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Tool Manufacture, Social Learning and Cognition in New Caledonian Crows

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Bird, I said, that fliest forever on New Caledonia's shore
That hast manufactured tools no other bird has dreamt before
Scientists have for centuries searched and thought and tried in vain
To reveal the dreary secrets that lie hidden in thy brain
Will there, will there come the hour when thy genius we'll explore?
Quoth the Raven: NEVERMORE!

H. Holzhaider, based on E.A. Poe, *The Raven*

Abstract

Wild New Caledonian crows are among the most sophisticated non-human tool manufacturers. In this thesis I investigate three important aspects related to the evolution and ontogeny of their tool skills that have not been studied in the wild before: the crows' social structure, the development of pandanus tool manufacture and use, and the crows' grasp of the functional properties of pandanus tools. My main methodological approach was to observe crows at feeding sites in their natural habitat on the island of Maré, New Caledonia.

The findings on NC crows' sociality revealed that they are one of the less social corvid species, with a social network size of probably less than 20 individuals. However, they have close, long-term relationships within their immediate family, which includes a partner and juveniles of up to two consecutive breeding seasons. Parental care is very extended, and juveniles may be tolerated and fed until 20 months old. The social structure of NC crows is likely to promote vertical transmission of tool skills while limiting the opportunity for horizontal transmission.

My developmental study showed that the ontogeny of wide pandanus tool manufacture is a lengthy process comparable to the development of tool use in primates, and that both individual and social learning are likely to play important roles. Juveniles do not reach adult proficiency until their second year of life and have ample opportunity to observe their parents' tool behaviour, while parents strongly scaffold the juveniles' learning environment. Exposure to parental tools might help juveniles form a mental template of functional tool design and thus facilitate the faithful transmission of local design traditions.

My experiments on NC crows' understanding of tool functionality showed that they do not strongly attend to the functional properties of pandanus tools. Instead, they appeared to solve tool problems through associative rules. In the wild, successful pandanus tool use is likely to rely on procedural knowledge of tool manufacture acquired during an individual's ontogeny.

Overall, my results suggest that New Caledonian crows' social structure and the mechanisms involved in the ontogeny of tool manufacture are suitable to support cumulative technological evolution that has been proposed to underlie the diversification of tool designs on New Caledonia's mainland Grande Terre.

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The research reported in this thesis was approved by the University of Auckland Animal Ethics committee (approvals R231 and R375) and complies with the laws of New Caledonia.

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1 Introduction

> ‘If men had wings and bore black feathers, few of them would be clever enough to be crows’
>
> (Rev. Henry Ward Beecher, ca. 1850)

Imagine the following, maybe familiar conversation: “Crows are really smart. Everyone knows that – just look at all the anecdotes and folk stories surrounding these birds! They can pull up fishing lines left in ice holes when flags signalled fish were hooked. And in Japan, they put nuts on the road, and then wait for cars to run over them and crack them open! Maybe they can even count!” “Yes, but chimpanzees are also great. They can use all kinds of tools, and there are even chimp cultures. Just look at how young chimps watch their mothers – they must surely copy them to learn to crack nuts! And aren’t we humans really rather arrogant and anthropocentric to assume that we are the only true cultural beings on this planet?”

Party talk – that reflects some of the major issues under discussion in the field of animal cognition over the past decades. For hundreds of years, animals were just that – animals. Early ethologists like Konrad Lorenz and Niko Tinbergen described animal behaviour as predominantly driven and controlled by an array of different instincts (Tinbergen 1951). More sophisticated behaviours and abilities – tool use and manufacture, recognition of the self, theory of mind, mental time travel, cumulative cultural evolution – were all thought to be exclusively human. Many of these claims have crumbled. A multitude of animals have been found to use tools, and a small number even manufacture tools (Beck 1980; St Amant & Horton 2008). Chimpanzees (*Pan troglodytes*) have passed tests of self-recognition in the laboratory (Gallup 1970; Povinelli et al. 1993). Several studies have shown that both chimpanzees (Hare et al. 2000, 2001) and corvids (Dally et al. 2005, 2007) know what conspecifics have or have not seen, which might enable them to 'tactically' deceive each other or human observers (Bugnyar & Kotrschal 2002; Hare et al. 2006). Western Scrub Jays (*Aphelocoma californica*) appear able to remember the 'what, where and when' while caching foods of different degradability (Clayton & Dickinson 1998; Clayton et al. 2003, 2007), and are even able to plan for the future (Raby et al. 2007).

What remains is an ongoing discussion about two main issues. First, what do animals understand about folk physics? That is, to what extent do animals grasp the physical properties of their world? Observations of behaviour in the wild often suggest that animals might understand the relevant functional properties of the tools they use. For example, chimpanzees in the Taï forest (Ivory Coast) use sticks of different lengths to suit different tasks: short sticks to extract marrow from bones and longer sticks to fish for termites or honey (Boesch & Boesch 1990). Individual chimpanzees have also been observed wedging a supporting stone under the anvil stone used for nut-cracking, thus stabilising the anvil and preventing nuts from rolling off (Matsuzawa 1994). However, observations in non-controlled natural settings are not sufficient to infer an understanding of unobservable physical forces like gravity. A multitude of experimental studies in the past decade have attempted to reveal what animals actually understand when they are engaged in object manipulations. In a series of experiments conducted by Povinelli and co-workers, chimpanzees failed to demonstrate an understanding of the causal properties of objects like shape, flexibility, contact and hooks (Povinelli 2000, but see Furlong et al. 2008; Bania et al. 2009). Other non-human primates could successfully use the relevance of certain features such as shape or colour to decide which tool to choose for certain tasks (cotton-top tamarins *Saguinus oedipus*: Hauser et al. 1999, 2002; Santos et al. 2003; vervet monkeys *Cercopithecus aethiops*: Santos et al. 2006; rhesus macaques *Macaca mulatta*: Santos et al. 2003).

A classic paradigm for exploring tool-related causal understanding is the trap-tube experiment, which requires subjects to extract a reward from a horizontal tube while avoiding a vertical trap in which they would lose the reward. However, the results from trap-tube experiments are not clear-cut and have caused much controversy among cognitive researchers.

Several primate species (Visalberghi & Limongelli 1994; Limongelli et al. 1995; Santos et al. 2006), as well as woodpecker finches (*Cactospiza pallida)* (Tebbich & Bshary 2004) are able to learn to avoid the trap, and under some conditions only do so when the trap is functional (Mulcahy & Call 2006). However, the subjects appeared to form (sometimes complex) associative rules based on observable features of the tasks, such as distance of the reward relative to the trap and the opening of the tube (Visalberghi & Limongelli 1994), but failed to understand unobservable causal mechanisms (Penn & Povinelli 2007). More recently, non-tool using rooks (*Corvus frugileus*) were tested on a modified, two-trap tube (Seed et al. 2006; Tebbich et al. 2007). The fact that one out of seven rooks that passed the initial problem was also successful in several transfer tasks is consistent with the idea that it understood the unobservable features of the task. It is equally possible, though, that this rook had abstracted a rule based on the observable features of the task, such as surface continuity and the inability of objects to pass through barriers (Seed et al. 2006). After decades of research, the debate about non-human animals' ability to causally understand the world they are living in is still ongoing. Such an ability would doubtlessly be very useful. An individual understanding tool functionality would likely be able to copy actions or tool designs more accurately than one that does not. Moreover, animals with an understanding of why a certain tool design works are likely to invent improvements with a higher frequency compared to animals relying on random modifications. The ability to understand physical relationships and functional properties of objects has therefore been claimed to be crucial for the development of cumulative technology (Nagell et al. 1993; Tomasello & Call 1997; Povinelli 2000). This leads to a second big issue in the field of animal behaviour and cognition – the evolution of culture.

Culture may be defined as socially learned behaviour patterns that are customary in some communities but absent in others, without ecological explanations for the variation (Whiten et al. 1999; Laland & Hoppitt 2003). Following this definition, culture can be found in a wide range of animals and contexts – from dialects in song birds (Marler & Tamura 1964; Mundinger 1980; Catchpole & Slater 1995) and humpback whales (*Megaptera novaeangliae*) (Noad et al. 2000; Rendell & Whitehead 2001), to the rich diversity of socially transmitted behaviours of non-human primates (chimpanzees: McGrew 1992; Whiten et al. 1999; orangutans *Pongo pygmaeus*: van Schaik et al. 2003; capuchin monkeys *Cebus sp.*: Ottoni & Izar 2008).

However, regardless of how complex these behaviours are, human culture is still quite different. One characteristic that appears to distinguish human culture from these non-human cultural variations is the incremental accumulation of improvements in traditions and artefacts over time (Boserup 1981; Boyd & Richerson 1996; Tomasello 2005). A fundamental prerequisite for this cumulative cultural or technological evolution is faithful social transmission. This can create a ratchet effect that ensures existing techniques or artefacts are preserved and faithfully reproduced until a new invention improves the current state (Tomasello et al. 1993). Some authors claim that only some very specific types of social learning, namely imitative learning, instructed learning and collaborative learning, can lead to true, human-like cultural transmission (Boyd & Richerson 1996; Tomasello 1999). While there is a relative consensus that cultural variation in many non-human species is socially transmitted, the exact mechanisms of this social transmission are the subject of much debate. For example, several studies have found no evidence that chimpanzees or orangutans can copy the actions of conspecifics in tasks that required them to use tools to retrieve food (Tomasello et al. 1987; Nagell et al. 1993; Call & Tomasello 1994; Myowa-Yamakoshi & Matsuzawa 1999). In contrast, Tomasello et al. (1993b) found that enculturated chimpanzees imitated at a similar level as 2.5 year old human children. Similarly, a review of 31 experiments with apes reported numerous cases of imitative behaviour and emulation, in which subjects copy the outcome of an action rather than its exact motor pattern (Whiten et al. 2004). In general, much of the socially learned behaviour of non-human primates appears to consist of a combination of different mechanisms like imitation, emulation and stimulus enhancement, augmented by individual trial and error learning (Fragaszy & Visalberghi 1996; Tomasello 1996).

Nevertheless, experimental work has now shown that chimpanzees can faithfully replicate foraging techniques along cultural transmission chains with the same fidelity as 3-year old children (Horner et al. 2006), and that multiple traditions are transmitted between groups (Whiten et al. 2007). Even when some individuals discovered an alternative method, they showed a conformity bias towards the approach predominantly used in their group. This conformity bias is considered by some to be a hallmark of human culture (Richerson & Boyd 2005). Whiten et al. (2009) therefore suggest that both human children and chimpanzees possess a range of social learning strategies, including both imitation and emulation, that are used according to context. Whether true cultural transmission is restricted to humans alone, and whether it necessarily relies on the mechanisms suggested by Tomasello and co-workers, remains therefore debatable.

However, despite the large number of examples of sophisticated behaviours like tool use and despite the possibility of cultural transmission, evidence of cumulative development in wild chimpanzee communities and other non-human animals is exceedingly rare (Boyd & Richerson 1996; Whiten 2005). Possibly the only well-documented example is song dialects in birds (Mundinger 1980; Baker & Cunningham 1985). Chimpanzees have challenged many aspects of tool use that have been claimed to be unique to humans, such as the possession of 'tool-kits' with different tools for different functions (Boesch et al. 2009), or the use of tools for underground food extraction (Sanz et al. 2004; Hernandez-Aguilar et al. 2007). Sanz et al. (2009) have documented that chimpanzee populations in the Congo Basin modify the tips of their termite-fishing probes into 'brushes' to improve their efficiency. However, evidence of ratchet-like technological evolution in animals is lacking.

Traditionally, research on animals' grasp of folk physics, on the existence of culture and on mechanisms of social learning has focused on non-human primates. More recently, however, another animal group has gained considerable attention: birds. In particular, corvids have demonstrated cognitive abilities that rival those of the great apes (Emery 2004; Tebbich et al. 2007; Emery & Clayton 2009; Seed et al. 2009; Taylor et al. 2009a, b; Bird & Emery, 2009, 2010). Like primates, corvid brains are significantly larger than would be predicted by their body size (Jerison 1973). Additionally, the relative size of the corvid forebrain is larger than in most other birds, particularly the nidopallium and mesopallium, which are thought to be functionally analogous to the mammalian prefrontal cortex (Rehkämper et al. 1991; Reiner et al. 2004). Even the lifestyle of many corvid species appears to be similar to non-human primates. For example, colonial species such as rooks or pinyon jays (*Gymnorhinus cyanocephalus*) live in complex, variable social groups reminiscent of the fission-fusion societies of chimpanzees (Clayton & Emery 2007). Like many primate species, corvids tend to be omnivorous, generalist foragers (Emery 2006). Several authors therefore suggest that similar socio-ecological pressures might have led to a convergent evolution of intelligence in corvids and apes (Emery & Clayton 2004b; Seed et al. 2009).

New Caledonian crows (*Corvus moneduloides*, NC crows hereafter) stand out in the corvid family for their exceptional ability to use and manufacture tools in the wild and in laboratory settings, for their complex problem solving skills, and for their extraordinarily large brains (Cnotka et al. 2008). In the wild, NC crows are one of the very few species that habitually manufacture tools, and the diversity of tools they manufacture is only matched by the great apes (chimpanzees: Whiten et al. 1999; orangutans: van Schaik et al. 2003). NC crows manufacture two main types of tools: stick tools made from twigs, leaf stems or other suitable material (Hunt & Gray 2002), and tools made from the barbed leaf edges of *Pandanus* sp. trees (pandanus tree hereafter) (Hunt & Gray 2004a).

Stick tools may be manufactured by simply breaking off twigs. Crows also use a much more complicated process to make hooked tools (Hunt 1996; Hunt & Gray 2004b). This process involves discarding a side twig that could have served as a tool, snapping off the potential tool below a junction, and sculpting a hook at the working end of the tool.

Pandanus tools are manufactured in three different designs: uniformly wide, uniformly narrow, and stepped (Hunt & Gray 2003). Stepped tools have the most complex design and combine the advantages of the other two: they are thin and flexible like narrow tools at the probing end, but sturdy and easy to grip like wide tools at the proximal end where held in the bill. Moreover, a pandanus tool is only functional after the final cut that removes it from the main leaf. Unlike the tools made by other species, pandanus tools cannot be made and used in a series of incremental functional steps. This led Hunt (2000b) to suggest that the shape of stepped tools is predetermined by a rule system before manufacture begins. After removal, an exact negative template, the counterpart, remains on the leaf, making it possible to reconstruct tools made from the tree up to four years ago (G.R. Hunt, personal communication). By documenting the shapes of over 5000 tools and counterparts at 21 sites across mainland Grande Terre and the island of Maré, Hunt and Gray (2003) showed that each design is characterised by a high degree of local standardisation. The specific design made at a site can remain the same for decades (G.R. Hunt, unpublished data), suggesting high fidelity transmission. Furthermore, the study revealed different, continuous and overlapping geographical distributions of the three tool designs. The increasing complexity of the tools, their geographical distribution and the lack of obvious ecological correlates has led to the suggestion that the diversification of pandanus tools arose through a process of cumulative technological evolution (Hunt & Gray 2003).

NC crows have also demonstrated exceptional abilities in laboratory settings. In 2002, ‘Betty’ impressed the scientific world by spontaneously bending wire into hook-like shapes to retrieve a bucket holding a reward from a perspex tube (Weir et al. 2002). In a follow-up experiment she developed novel strategies to unbend aluminium strips into functional tools (Weir & Kacelnik 2006). While the exact cognitive mechanisms behind this remarkable behaviour remained unclear, it showed that NC crows can modify tools in response to a specific need. More relevant to crows’ tool behaviour in the wild, Chappell and Kacelnik (2002, 2004) also demonstrated that NC crows can choose tools of appropriate length and manufacture tools of appropriate diameter to solve a task. In a recent series of experiments aimed to further explore their cognitive potential, NC crows were shown to rival non-human primates in meta-tool tasks (Köhler 1925; Mulcahy et al. 2005; Taylor et al. 2007; Wimpenny et al. 2009). In experiments using the trap tube paradigm, coupled with a transfer task (the 'trap table'), the crows demonstrated causal reasoning based on an understanding of object-object interactions (Taylor et al. 2009a, b).

The remarkable skills of NC crows suggest that they are an ideal species to examine the links between tool manufacture, social learning and cognition. However, until very recently almost every aspect in the lives of NC crows that might be related to tool manufacture, tool use and the development and transmission of these abilities was unknown. With the exception of a scarce handful of observations in the wild (Hannecart & Letocart 1980; Hunt 2000a; Kenward et al. 2004), the social organisation of NC crows was unknown. The breeding behaviour and extent of parental care was unknown. While there are several investigations on the crows' understanding and use of stick tools both in the wild and in the laboratory (Hunt 2000a; Chappell & Kacelnik 2002, 2004; Hunt et al. 2006), the apparently sophisticated use of barbed pandanus tools in the wild remained largely un-investigated. Most importantly, nothing at all was known about the development of pandanus tool skills in the wild, and how it might have led to the existence and geographical distribution of the different tool designs found on Grande Terre. Based on observations of four hand-raised individuals in the laboratory, Kenward et al. (2005, 2006) suggested that proficient stick tool use and possibly even basic pandanus tool manufacture might develop without social input. They cautioned, however, that social learning might be involved in the development of the more complex stepped tool manufacture. But what about the actual processes that lead to proficient tool manufacture and use in the wild? Do young crows even have the opportunity to watch their parents during tool manufacture and use? How long does the development of proficient tool manufacture take? Do wild young crows manufacture functional, adult-like wide pandanus tools straight away and without social input, as Kenward and colleagues' work suggests? This thesis attempts to answer some of these fundamental 'unknowns'. To accomplish this aim, I studied wild NC crows in their natural habitat on the island of Maré, New Caledonia. With the exception of the experiments in Chapter 4, which were partly conducted with short-term captive crows in an outdoor aviary, my focus lies on behavioural observations of crows at feeding sites in their natural habitat to achieve maximal ecological validity.

In Chapter 2 I investigated the social structure of NC crows to assess how the lifestyle of this species might have influenced the development of their remarkable skills. One theory attempting to explain how large brains and complex cognition have evolved is broadly known as the social intelligence hypothesis. This hypothesis claims that the challenges of living in large, complex social groups, such as the need to recognise individuals, track their relationships, deceive and co-operate with each other were the main forces that have driven the evolution of intelligence (Humphrey 1976; Byrne & Whiten 1988; Whiten & Byrne 1997; Dunbar 1998). The social intelligence hypothesis is supported by several studies that link brain size with social group size in primates (Dunbar 1992) and other vertebrates (Barton & Dunbar 1997; Dunbar & Bever 1998; Marino 2002; Connor 2007). Furthermore, Silk (2007) provides evidence that social intelligence can be adaptive by leading to significantly increased fitness and offspring survival in several mammalian species. Following these results we might expect that NC crows live in complex social groups. However, no close correlation between group size and encephalization has been found for birds (Beauchamp & Fernández-Juricic 2004; Emery

2004; Iwaniuk & Arnold 2004). Yet corvids have developed similar cognitive abilities to non-human primates. Emery et al. (2007) therefore suggest that in birds, the quality of the social relationships (such as life-long pair bonding and shared parental care) is more important in predicting brain size than group size. In Chapter 2, I attempt to judge the social complexity of NC crows by estimating their social network size based on tolerance to other crows at feeding sites in their natural habitat. Based on these results, I discuss the likelihood for vertical and horizontal transmission of tool skills. Furthermore, I describe the year-round family structure and some aspects of the breeding behaviour of NC crows.

In Chapter 3 I address the core question of this thesis: how do young NC crows learn to manufacture and use pandanus tools in the wild? The existence and geographical distribution of the different pandanus tool designs on Grande Terre and the high degree of local standardization suggest the transmission of tool manufacture skills through high fidelity social learning. However, when Kenward et al. (2005) investigated the emergence of stick tool use in four hand-raised individuals, they found that basic stick tool use can develop without any social input. Moreover, the crows were able to produce rough strips of pandanus leaves and use them to extract meat at an early age on their first exposure to the material, suggesting that even basic pandanus tool manufacture might develop independently of social learning (Kenward et al. 2006). The rapid development of the crows' tool skills reported in these studies is in strong contrast to the lengthy development of complex tool use in other species. Wild chimpanzees for example take many years to develop skills like nut cracking or ant dipping (Nishida & Hiraiwa 1982; Inoue-Nakamura & Matsuzawa 1997; Humle 2006). This discrepancy suggests that laboratory observations of a small number of captive, hand-raised birds are not sufficient to explore all the relevant influences leading to complex tool behaviour in the wild. I therefore documented the development of wide pandanus tool manufacture and use in six NC crow juveniles that regularly visited feeding sites in their natural habitat on Maré together with their parents and siblings.

In Chapter 4 I focus on one particular tool behaviour in order to assess NC crows' grasp of the folk physics involved in the tools they habitually manufacture in the wild: the use of naturally barbed pandanus tools. NC crows utilise the barbs along one edge of these tools to extract prey out of the narrow crevasses between the leaves of pandanus trees (my personal observations). Because the barbs run along the tool edge at around a 65-degree angle, they are only functional as hooks when used pointing upwards towards the holding end. Adult crows virtually always use pandanus tools this way and extract prey (or meat from logs at feeding sites) with careful, deliberate movements that leave little doubt that they are aware of the existence and function of the barbs. Betty's wire bending in the laboratory (Weir et al. 2002) also suggested a possible understanding of hooks. I therefore designed two experiments to assess: (1) whether the crows attended to the directionality of the barbs and (2) whether they recognised the barbs as a crucial functional feature of the pandanus tools. In Experiment 1 I presented crows with a tool in a baited vertical hole. The tool was either in a functional position (barbs pointing upwards) or in a non-functional position (barbs pointing downwards). If the crows recognised the direction of the barbs as functionally important, they should use the tool as it was presented in the functional position, but turn it around when (and only when) it was in the non-functional position. If crows acted this way, it would be consistent with them understanding the functional properties of the barbs, in particular their directionality. Latencies to flipping and other reactions would further indicate whether the behaviour was based on strategies acquired during the experiment or on previous knowledge about the functionality of barbs. To incorporate tool observations in more natural conditions, I documented the orientation in which two free-living crows picked up and used pandanus tools that had been dropped at feeding tables.

In Experiment 2 I investigated whether the crows associated the existence of barbs with tool functionality by giving them a choice between a barbed tool and one where the barbs had been removed. Failure to reliably choose the barbed tool would suggest that tool using strategies are based on trial and error learning, depending whether a given tool is currently functional or not.

In the final chapter I summarise my results and discuss how they can help explain the evolution and geographical distribution of pandanus tool designs on Grande Terre. I suggest further lines of research that could shed more light on remaining questions, particularly on the development of the most complex variety of pandanus tools – the stepped design. Finally, I discuss how my findings on the crows' understanding of the properties of their tools fit into the results of recent experimental work suggesting that NC crows can reason causally about interactions between objects.

2 The Social Structure of New Caledonian Crows[1]

Abstract

Two main hypotheses have been proposed to explain how complex cognitive abilities have evolved: the social intelligence hypothesis and the technical intelligence hypothesis. New Caledonian crows have impressive tool manufacturing and using skills in the wild, and captive birds have displayed exceptional cognitive abilities in experimental situations. However, their social system is largely unknown. In this study I investigated how the social structure of NC crows might have assisted the development of their cognitive skills. I observed crows in their natural habitat on the island of Maré and estimated their social network size based on tolerance to family and non-family members at feeding sites. My findings suggest that NC crows are not a highly social corvid species. Their core unit is the immediate family consisting of a pair and juveniles from up to two consecutive breeding years. Pairs stay together all year round and are closely accompanied by juveniles during their first year of life. Juveniles are tolerated and may be fed until well into their second year. NC crows predominantly shared feeding sites with immediate family. Of the non-family members tolerated, juveniles were over represented. The crows' social network size appeared to be limited to approximately 16 individuals, including immediate family. The main mechanism for any social transmission in foraging skills is likely to be vertical (from parents to offspring), with only limited opportunity for horizontal transmission. The social organisation I found on Maré is consistent with the idea that NC crows' multiple pandanus tool designs on mainland Grande Terre are an example of cumulative technological evolution.

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[1] Based upon Holzhaider, J. C., Sibley, M., Taylor, A. H., Singh, J. P., Gray, R. D., & Hunt, G. R, (in press). The social system of New Caledonian crows. *Animal Behaviour.*

Introduction

Two main hypotheses have been proposed to explain how complex cognitive abilities have evolved. The social intelligence hypothesis claims that social pressures have driven the evolution of a flexible, intelligent mind (Byrne & Whiten 1988; Whiten & Byrne 1997; Dunbar 1998). This hypothesis is supported by many findings that correlate brain size with group size and social complexity in primates and a range of non-primate mammals (Byrne & Bates 2007). However, no clear correlation has been found between avian brain size and sociality (Emery et al. 2007). Emery et al. therefore suggest that in birds the type and quality of social relationships might be more important factors for predicting brain size than group size. In contrast to the social intelligence hypothesis, the technical intelligence hypothesis states that ecological factors, in particular the need for extractive foraging, helped drive brain expansion and the associated increase in cognitive abilities (Byrne 1997). This theory is supported by findings that correlate the size of forebrain areas of both birds and primates with flexible and innovative non-social behaviours such as tool use (Lefebvre & Sol 2008). The two theories are not necessarily mutually exclusive (Sterelny 2007), but might complement each other. In fact, the technical intelligence hypothesis was proposed as a mechanism that might work alongside the social intelligence hypothesis to drive the evolution of intelligence (Byrne 1997).

Corvids are renowned for their innovative behaviour, relatively large brains and general intelligence (Emery 2004; Emery & Clayton 2004a, b). For example, New Caledonian crows appear to have the most complex tool manufacturing abilities amongst non-human animals including primates (Hunt 1996; Hunt & Gray 2004a, b). Hunt and Gray (2003) suggested that the diversification of the designs of tools that NC crows make from pandanus leaves on mainland Grande Terre might be the result of cumulative technological evolution. While tool use is not necessarily indicative of advanced cognitive abilities (Beck 1980; Hansell & Ruxton 2008; Emery & Clayton 2009), NC crows have demonstrated impressive abilities when solving complex physical problems in captivity. They can modify novel tool material in appropriate ways (Weir et al. 2002; Weir & Kacelnik 2006), spontaneously solve a novel metatool task (Taylor et al. 2007) and appear to reason causally about interactions between objects (Taylor et al. 2009a, b). Their metatool performance rivals that of the great apes (Köhler 1925; Mulcahy et al. 2005). With the possible exception of rooks (Bird & Emery 2009) they appear to be the only non-human species known to have solved problems requiring tool use through causal reasoning (Martin-Ordas et al. 2008; Seed et al. 2009; Taylor et al. 2009a, b). Furthermore, NC crows also possess relatively large brains compared to other birds, including several corvid species (Cnotka et al. 2008). However, very little is known about their social structure. Early observations suggested that crows live mostly in small family groups (Hunt 2000a; Kenward et al. 2004). Hunt (2000a) observed a nutritionally independent juvenile moving around with adults and suggested that the 30 or more crows he observed in a tree at the Sarraméa site on Grande Terre was a temporary aggregation of small groups. Kenward et al. (2004) saw NC crows flying above the canopy on Grande Terre in groups of typically three to four and captured crows in small mixed-sex groups, which is consistent with the idea that NC crows mostly live in small family groups. A more intensive study on the island of Maré showed that juveniles follow their parents for at least one year and are frequently fed during this time (Holzhaider et al. 2010). However, no one has undertaken a detailed field study with individually marked NC crows to investigate their social structure.

The family Corvidae displays a very broad range of social organisation. While the core unit in all species is the life-long mated pair that usually remains together throughout the year, social organisation ranges from solitary pairs that nest within a large territory, like common ravens (*Corvus corax*) (Heinrich 1999), to highly social species such as the pinyon jay which lives in stable groups of up to 500 birds and breeds cooperatively within the colony (Marzluff & Balda 1989). If, as Hunt (2000a) and Kenward et al. (2004) suggest, NC crows live mostly in small family units it would place them at the lower end of corvid social complexity and increase the possibility that technical intelligence had a role in the evolution of their impressive cognitive abilities. In this study, I present the results of four consecutive years of observations on a population of individually colour-banded NC crows on the island of Maré, New Caledonia. I describe the structure of nine target families, their breeding behaviour and the tolerance of individual birds to other NC crows at feeding sites in the crows' natural habitat.

Methods

The study was carried out on Maré, about 5km inland from Wabao village. Crows were observed from August-December 2003, June-December 2004 and in most months in 2005 (January-May, July and October-December) and 2006 (January-May, August and October-December). The study area consisted of ca. 1.5 km^2 of primary and secondary rain forest. Forest areas were interspersed with garden patches where local villagers grew fruit and vegetables. These gardens still supported many dead, upright trees and were usually used for two consecutive years before they became overgrown. Crows foraged in both forest and garden patches.

I documented the social structure of nine target families at the study site where over 100 crows had been individually colour-banded between 2003 and 2006 (Table 2.1). Adult crows were being recorded as partners if they were observed together at any of the following activities: courtship feeding, nesting, and feeding the same juvenile. Parent-juvenile relationships were identified by parental feeding, intensive begging and continuous following of an adult by a juvenile.

Observations were made at 24 feeding tables that were distributed in the forest and gardens (Figure 2.1). Feeding tables were ca. 1m above the ground and made out of wood found in the vicinity. The tables were generally provided with fresh papaya and pieces of meat. The meat was put in holes that had been drilled into dead logs, and could only be extracted with tools. A pandanus tree was normally attached to a table to provide the opportunity for pandanus tool manufacture. Several tables were usually baited at the same time.

Whenever one or more crows landed on a table, the time of the visit and the identity of the present individuals were recorded. Visits were separated by at least two minutes when no crow was on the table. Visits were recorded in notebooks, videotaped with a handheld camera, or videotaped remotely in conjunction with a motion detector (Wachit VMD-19M video motion detector, Farco Technologies, New Zealand). Whenever a target bird was observed away from tables we also recorded the location, time and whether a family member was present (i.e. less than ca. 100m away).

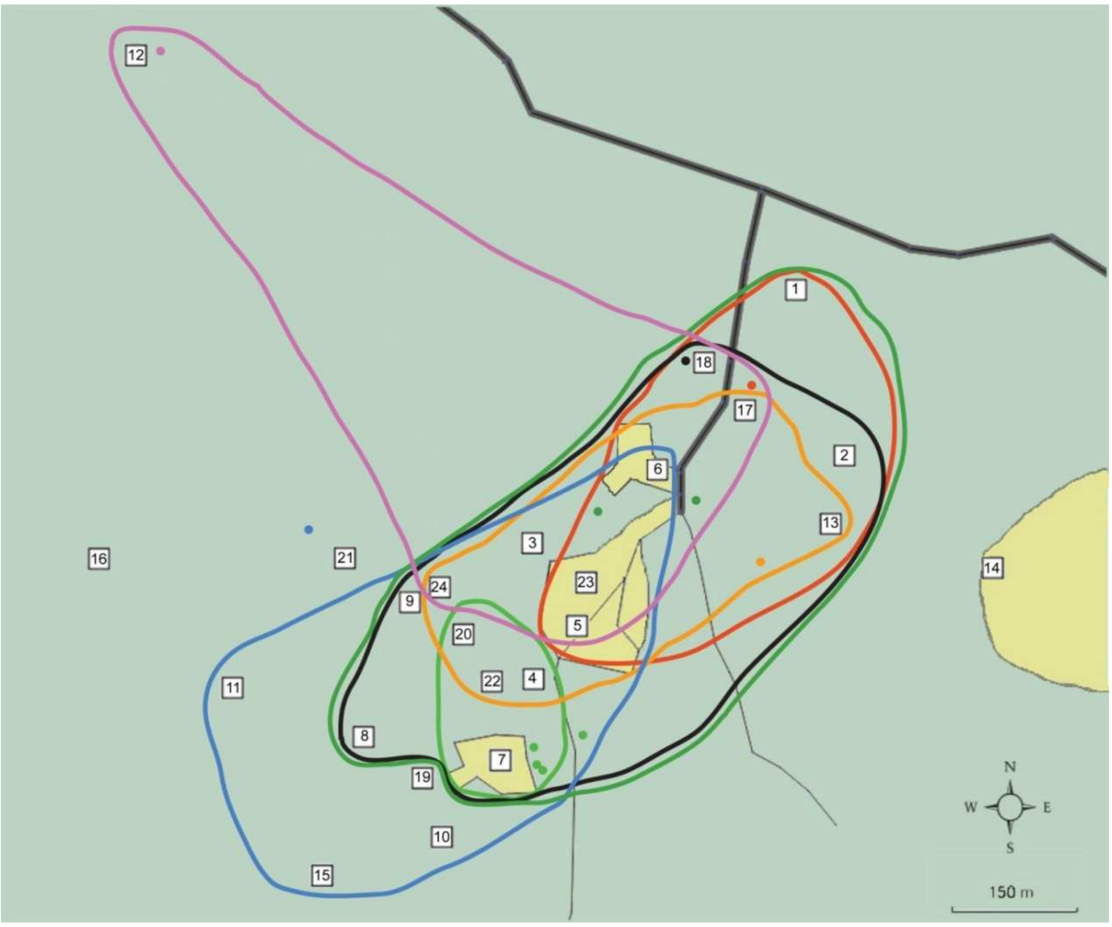

Figure 2.1. Map of study area, distribution of tables and nests, and foraging areas of target families. ☐ Feeding table —— foraging area of family ● nest site of family. Dark green areas are forest, light green areas are garden patches. Colour code:

—— Family 1 —— Family 2 —— Family 3 —— Family 4

—— Family 5 —— Family 6 —— Family 7

Table 2.1. Details of target families

	Crow	Status	Sex	Hatched	Fledged	Banding date	Band number
Family 1	Epi[x]	Adult	m	-	-	23/09/2003	H 12176
	Pandora	Adult	f	-	-	unbanded	-
	Primo	Juvenile	m	02/12/2004*	01/01/2005	30/12/2004	H 33110
Family 2	Abraxas	Adult	m	-	-	21/09/2003	H 12166
	Pandora	Adult	f	-	-	unbanded	-
	Yor	Juvenile	m	13/11/2005*	14/12/2006	13/12/2006	n. recorded
Family 3	Adam	Adult	m	-	-	23/07/2004	H 12182
	Godot	Adult	f	-	-	24/07/2004	H 12190
	Cain	Juvenile	m	06/11/2005*	06/12/2005*	14/02/2006	H 29765
	Abel	Juvenile	m	06/11/2005*	06/12/2005*	14/02/2006	H 29755
Family 4	Klaus	Adult	m	-	-	14/09/2003	H 12154
	Maui	Adult	f	-	-	14/09/2003	H 12152
	Bo	Juvenile	f	06/11/2005*	06/12/2005*	16/02/2006	H 29757
Family 5	Artus	Adult	m			20/09/2003	H 12162
	Morgan	Adult	f			02/12/2005	H 29751
	Moro	Juvenile	m	06/11/2005*	06/12/2005*	unbanded	-
Family 6	Snoopy	Adult	m			14/09/2003	H 12155
	Doro	Adult	f			14/09/2003	H 12156
	Brando	Juvenile	m	Dec 2003#	Jan 2004#	23/07/2004	H 12187
	Orange	Juvenile	f	07/12/2004*	02/01/2005	30/12/2004	H 33111
Family 7	-/wy	Adult	m			23/09/2003	H 12175
	gw/b	Adult	f			18/10/2004	H 33109
	b/r	Juvenile	m	Dec 2003#	Jan 2004#	24/07/2004	H 12197
	r/o	Juvenile	m	Dec 2003#	Jan 2004#	18/08/2004	H 12191
Family 8	y/g	Adult	m	-	-	20/09/2003	H 12164
	g/y	Adult	f	-	-	04/08/2005	H 33134
	Twiggy	Juvenile	m	Dec 2004#	Jan 2005#	04/08/2005	H 33133
Family 9	r/y	Adult	m			19/09/2003	H 12159
	b/g	Adult	f			19/09/2003	H 12160

[x] died in late 2004 before Primo fledged. * Date estimated from observations at the nest.

[#] Date estimated from mouth colouring and behaviour at capture. m = male, f = female.

To document whether pairs ($N = 9$) were travelling together year round I used observations at and away from feeding tables. I counted all the days on which each target male was observed and recorded the number of days his partner was with him. If a target male was observed in more than one year I averaged the number of days observed for each month across years. For example, if a male was observed on 15 days in January 2005 and on 5 days in January 2006, the average number of days in January across the two years was 10. I then took the average of all target males for each month of the year. I applied the same procedure to document the target juveniles travelling with their families in their first and second year of life.

To obtain a measure of social network size I analysed all videotaped visits of target males to feeding tables and recorded the number of both family members and non-family members tolerated on the table by each male in each year. Family members could be the partner and any offspring. I recorded that a target male tolerated another bird if he allowed it to share the table or attached pandanus tree without displacing it or leaving the table upon the other bird's arrival. I then added all visits of all target males for each month of all study years. In this analysis I only included males that had been observed at tables on at least 20 visits in any one year. Only Families 1-6 met this criterion. I applied the same procedure to assess the opportunity of first year juveniles to observe tool use and manufacture at tables.

Social transmission in a population may be from parents and close family to offspring, or between unrelated individuals. For transmission between unrelated individuals, some authors distinguish between horizontal transmission (between peers, i.e. individuals from the same (F1) generation) and oblique transmission (between non-related individuals of different generations) (Boyd & Richerson 1985; Findlay et al. 1989; Allison

1992). My objective was to determine the extent to which juveniles may socially learn about tool behaviour from close family members or from non-related individuals. I therefore defined all potential transmission to a juvenile from parents and previous year siblings as ‘vertical’, and all potential transmission between non-related individuals as ‘horizontal’ (Cavalli-Sforza & Feldman 1981; Bisin & Verdier 1998). Following these definitions, a juvenile had the chance to learn tool skills via vertical transmission when it shared a table with a parent or sibling. It had the chance to learn tool skills via horizontal transmission when it shared a table with a non-related NC crow. In 2006, two same brood siblings (Cain and Abel) shared tables in 93 visits without the presence of any other crow. As the transmission of tool skills between inexperienced same-brood siblings appears unlikely to play an important role I excluded these visits from the analyses.

In late 2004 we also observed four breeding pairs (Families 1, 4, 6, and 9) at their respective nests. To make observations at nests, hides were set up at a distance of ca. 10-20m. For better visual access to the nests the hides were raised on 2-4m high platforms built out of natural material. To minimise disturbance of the breeding pairs each nest was only observed every two to three days for several hours. Observers attempted to enter and leave the hide only when the breeding pair was absent from the nest. During incubation and after hatching we recorded the amount of time each parent spent sitting on the nest and whether the male or the female fed the juvenile(s). To estimate the maximum duration of parental feeding post fledging I recorded the approximate age (months) of each juvenile of Families 1-9 when it was last observed being fed by an adult. For this analysis I only included families in which both the juvenile and its parents were observed for at least 12 months post fledging.

Results

Breeding and Parental Care

At the study site the breeding period started around November, when both partners contributed to nest building. In 2004, the nests of the four breeding pairs were observed for an average of 21.4 hours each (SE = 3.24, *N* = 4) from the time incubation started until juveniles fledged or the nest was deserted. Nests were built ca. 3-8m above ground, but still well below the canopy. Females laid 2-3 eggs and incubation lasted ca. 18 days (X ± SE = 17.67 ± 0.33, *N* = 3; exact data on incubation period is missing for Family 9). Only the females incubated and brooded the chicks, while the male fed the female regularly on or close to the nest. From a total of nine chicks that were hatched by the four pairs, only two survived to fledging (22%). The two surviving chicks left the nest 26 and 30 days after hatching. Reasons for chick mortality appeared to be adverse weather conditions and predation. In one case I observed a goshawk (*Accipiter sp.*) attack a nest and kill an almost fledged juvenile. One pair built a replacement nest and started incubating after both chicks of the first brood had died, but the second nest also failed. Nests were also found in 2003 (Family 4) and 2005 (Families 2, 4 and 6). Consecutive nests of the same family (either in the same or in different years) were never further than 100m apart.

Juveniles were fed by both parents. Although parental feeding frequency clearly declined after about six months (Holzhaider et al. 2010), juveniles were fed infrequently until at least the beginning of the next breeding season. The average age of a juvenile when it was last observed being fed was 12.6 months (SE = 2.4, *N* = 5). I observed three juveniles over 12 months from different families begging vigorously and subsequently being fed (at 14, 14 and 20 months of age). At 20 months, Brando was still being fed by both parents even though they were raising a new juvenile. I never observed any bird other than the biological parents feed a juvenile or contribute directly in any other way to their upbringing.

Pair Bonding and Family Structure

Five of the nine banded pairs stayed together for at least two consecutive breeding seasons. Two pairs (Klaus/Maui and Abraxas/Pandora) bred together over five consecutive years (from 2003-2007 and 2005-2009, respectively). The pairs remained in the same foraging area and visited the same feeding tables for the entire study period. In 2005, Pandora paired with a new partner (Abraxas) several months after her former partner had probably been killed by a goshawk in December 2004. Although I never observed Abraxas feeding his ‘stepson’ Primo, he tolerated him on feeding tables and rarely showed any antagonistic behaviour towards him. For this reason I treated Abraxas and Primo as ‘family members’ in all following analyses. Partners were observed travelling together year round (Figure 2.2).

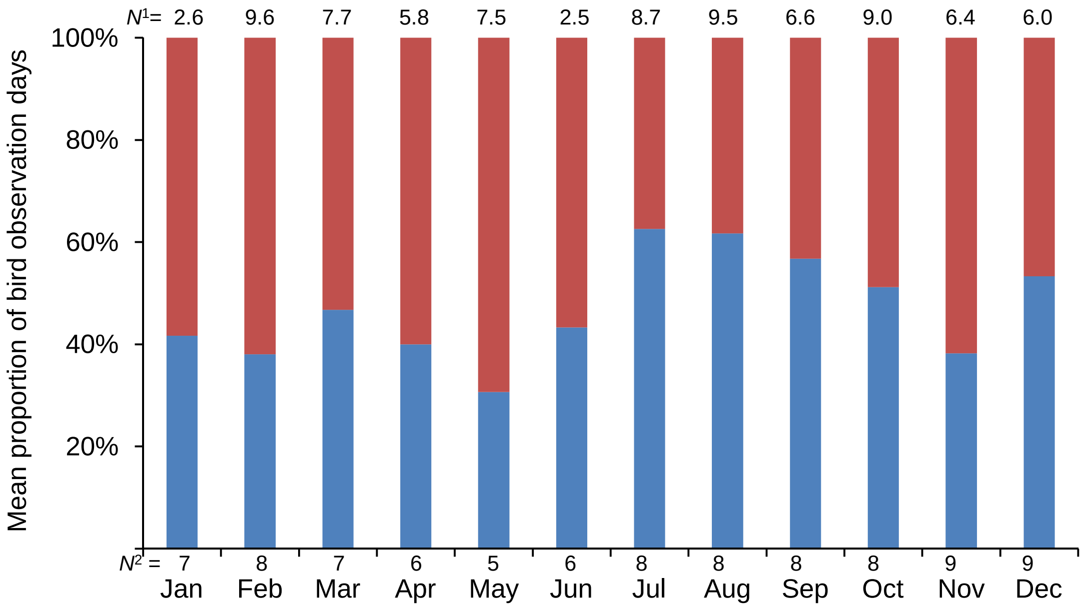

Figure 2.2. Association of target males with their partners. Target males associated with their partners year round. The y-axis gives the mean proportion of bird observation days on which target males were seen with their partner. N^1 = mean bird observation days per month. N^2 = number of target males observed in each month.

🟦 Proportion of days seen with partner 🟥 Proportion of days seen without partner

As females tend to be reticent and visited tables less frequently than males (JCH unpublished data), I probably underestimated the amount of time pairs travelled together. Juveniles stayed with their parents after fledging for up to 21 months (Figure 2.3). The proportion of time juveniles spent with their parents decreased substantially during the next breeding season when juveniles were a year old. After the breeding season they were observed with their parents more frequently again and travelled together for several more months. The lack of observations of second year juveniles with their parents in June is most likely due to the low number of observations during that month (juveniles were only observed on four days in June in the study years 2005 and 2006).

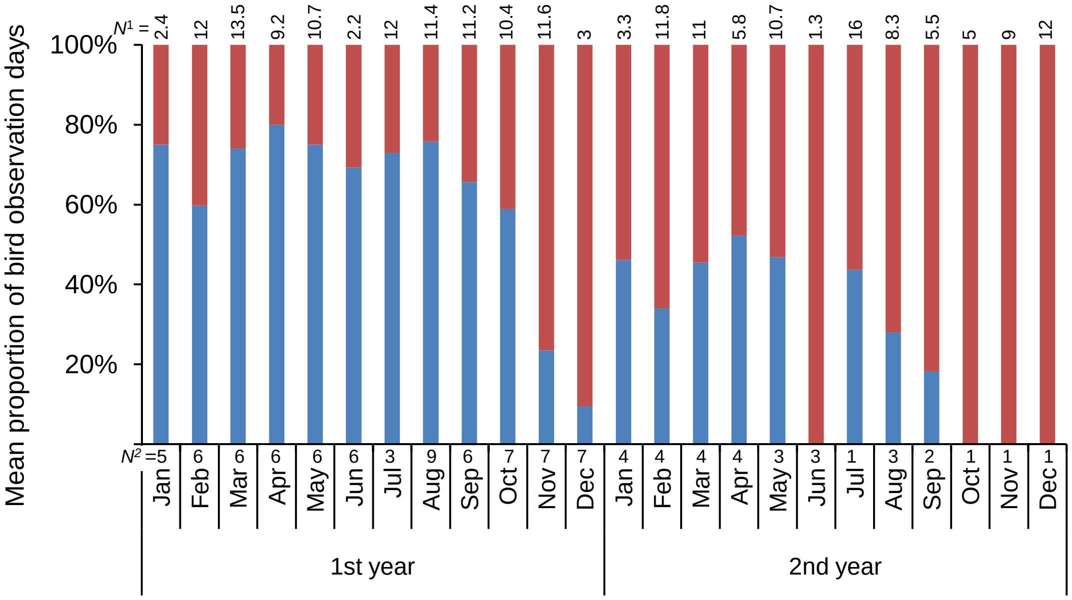

Figure 2.3. Associations of juveniles with their parents. Juveniles travel with their parents during the first two years of their lives. The y-axis gives the mean proportion of bird observation days on which juveniles were seen with one or both parents. N^1 = mean bird observation days per month. N^2 = number of juveniles observed in each month

🟦 Proportion of days seen with parent 🟥 Proportion of days seen without parent

Adult Tolerance at Feeding Tables

Each target male and his family visited up to 14 different feeding tables, and most tables were visited by several different families (Figure 2.1). We videotaped 966 visits by the six target males that visited feeding tables at least 20 times in any one year (Figure 2.4). In 505 of these visits the males shared the table with other crows. In the majority of these 505 visits (82.2%) the tolerated birds were exclusively family members (partner and/or juveniles), and family members were present with other NC crows in another 35 visits (6.9%). Target males shared the tables only with non-family crows in 55 visits (10.9%).

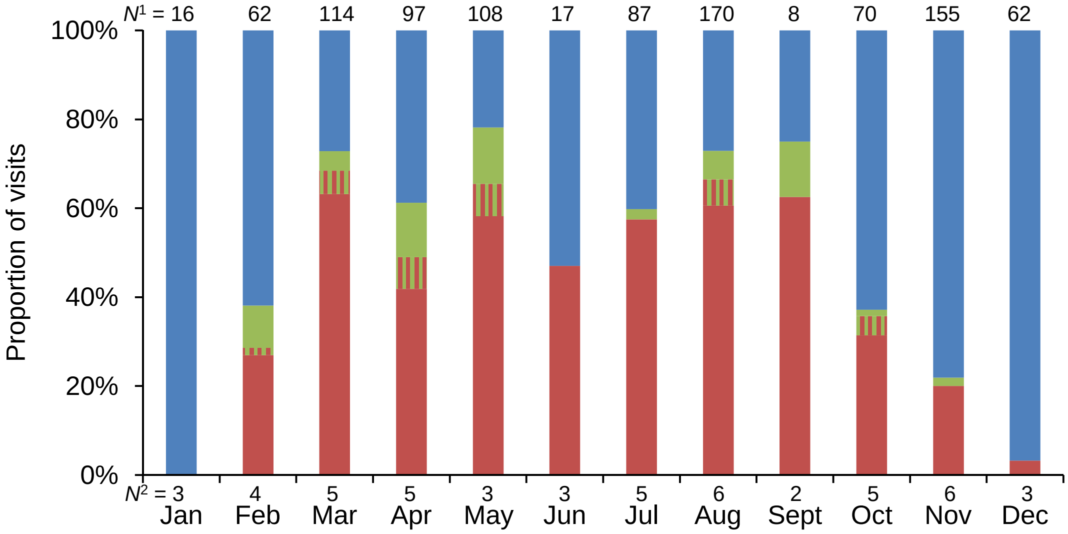

Figure 2.4. Tolerance of other birds by six target males at feeding tables.

Family members are more frequently tolerated than non-family members. N^1 = total number of visits by all six target males. N^2 = number of target males observed in each month.

Crows tolerated at table: 🟦 None 🟥 Family only ▨ Family + Others 🟩 Others only

Target males shared tables with up to 13 different individuals in any one year (X ± SE = 5.8 ± 1.6, $N = 6$, Table 2.2). The maximum number of different non-family crows tolerated in any one year was 11 (X ± SE = 3.7 ± 1.5, $N = 6$). While juveniles represented only 29% of the non-family crows (5 juveniles vs. 12 adults) they shared tables with the target males in 50% of visits (45 out of 90 visits). This is significantly more than would have been expected from the juvenile/adult ratio (chi-square test, $\chi^2 = 5.41$, df = 1, $p = 0.02$, $N = 90$).

The six target males above visited tables alone 465 times (48% of 966 visits). During the breeding period and in the first month after juveniles fledged (November–January) each male shared tables with other NC crows less frequently than during the rest of the year. The probability for all males behaving this way is $(0.5)^6 = 0.016$.

Table 2.2. Social contacts tolerated by six target males at feeding tables

Family	Target male	Year	No. of visits at tables	No. of non-family members tolerated at tables	No. of family members tolerated at tables	Total No. of individuals tolerated at tables	Mean No. of individuals tolerated at tables
1	Epi	2004	92	0	1	1	1.0
2	Abraxas	2005	126	1	2	3	6.5
		2006	150	7	3	10	
3	Adam	2006	143	9	3	12	12.0
4	Klaus	2004	30	0	1	1	4.0
		2005	24	1	1	2	
		2006	71	7	2	9	
5	Artus	2004	38	2	1	3	8.0
		2006	194	11	2	13	
6	Snoopy	2005	65	0	3	3	3.0

Opportunities for Social Transmission at Tables

We videotaped 853 visits of seven young juveniles (<1 year old) to feeding tables (Figure 2.5). In 404 of the 853 visits the juveniles shared the table with other crows. In the majority of these 404 visits (81.2%) the accompanying birds were parents and/or older siblings, which provided the potential opportunity for the vertical transmission of tool skills. Older siblings were only present in a total of 19 visits. In 10 of these 19 visits at least one parent was also present. This indicates that the main opportunity for vertical transmission is between parents and offspring. The juveniles shared a table with non-family crows on 100 visits (24.7%), which provided the potential opportunity for the horizontal transmission of tool skills.

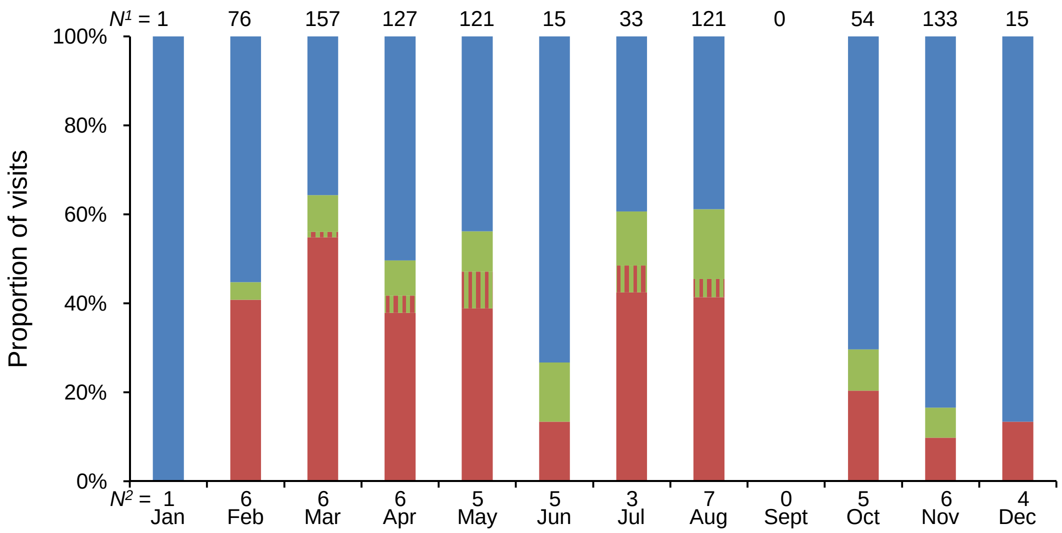

Figure 2.5. First year juveniles' opportunities for social learning from sharing feeding tables. Juveniles have much more opportunity to learn from their immediate family (vertical transmission). N^1 = total number of visits by all first year juveniles. N^2 = number of first year juveniles observed in each month. Juveniles visited table with:

🟦 None 🟥 Family only (vertical transm.) ▥ Family + Others 🟩 Others only (horizontal transm.)

Discussion

My findings confirm the preliminary observations of Hunt (2000a) and Kenward et al. (2004) suggesting that New Caledonian crows live mostly in small family units. I found that these family units are based on long lasting pair bonds that are maintained year round. Each family unit at the study site appeared to interact with only a small proportion of the resident crow population, while sharing largely overlapping foraging areas. Furthermore, juvenile NC crows lived closely with their parents up to the following breeding season. Occasional parental feeding continued well into a juvenile’s second year of life. The type of social system I found in NC crows on Maré has both similarities and differences with known social systems in other corvids.

Many authors have used group size as a measure of social intelligence and complexity (e.g. Dunbar 1992, 1998; Marino 2002; Connor 2007). However, group size alone appears to be a poor predictor for social complexity (Beauchamp & Fernández-Juricic 2004; Holekamp 2007). This seems to be particularly true for birds (Emery et al. 2007). Social network size, which may be defined through the number of individuals having social relationships with each other (Wey et al. 2008), might therefore be a better measure to assess social complexity. Social relationships might include interactions like grooming, agonistic interactions, food sharing and others. The overlapping foraging areas of the study families (Figure 2.1) show that families do not defend exclusive territories. Aggressive encounters between non-family birds were rare and almost exclusively restricted to feeding tables where individuals or families would displace one another. We also observed the families and other individuals of our banded population visiting and feeding in garden patches in loose groups without aggressive interactions, and each crow was likely to encounter a considerable number of different conspecifics on a daily basis.

Nevertheless, we rarely saw direct social interactions between individuals of these aggregations, suggesting that an individual's social network does not include all of them. Crows do, however, occasionally share feeding tables. To obtain a measure of NC crows' social network size I therefore used tolerance at feeding tables. Feeding tables were highly desirable food sources because they were baited regularly with meat and papaya. Any other bird on the table is therefore a competitor for the food. Food sharing has been suggested to play an important role in the development of social bonds in other corvids such as jackdaws (*Corvus monedula*) (von Bayern et al. 2007) and rooks (Emery et al. 2007). Similarly, many primate species generally share food only with individuals they have established social relationships with (de Waal 1989; Stevens & Gilby 2004). To tolerate a conspecific on the table I would therefore expect a crow to individually 'know' this bird and remember social interactions they had in the past.

Target males tolerated up to 11 different non-family individuals on tables during the course of a year (Table 2.2). Adding immediate family (a partner and up to two juveniles from each of two consecutive breeding seasons), an adult male at our study site might tolerate a maximum of around 16 individuals. However, a social network would also include contacts based on antagonistic interactions between individuals. This might have resulted in crows being close to a feeding table but avoiding it because of intolerance to certain individuals or families. Unfortunately, such cases are by their nature very difficult to assess and are not accounted for in this study. Non-related first year juveniles were tolerated more often than would have been predicted from their numbers in the study group. The reason for this might be that juveniles commonly display submissively when in close proximity to a non-family adult and are therefore less of a potential threat. As a result, adult males might tolerate them without having previously built a social relationship with them.

My findings suggest that the social complexity of the NC crows is low when compared to many other corvids. For example, rooks can nest within colonies of hundreds of pairs and may assemble in winter roosts of tens of thousands of individuals (Clayton & Emery 2007). While they are unlikely to interact closely with all individuals of these huge groups, they clearly have more social contacts than do NC crows. The same applies to pinyon jays that live in permanent flocks of 50–500 individuals (Balda & Bateman 1971; Marzluff & Balda 1989). In the highly social Mexican jay (*Aphelocoma ultramarina*), two adult pairs typically share a territory with numerous non-breeding helpers, all of whom participate in feeding the juveniles and defending the territory (Clayton & Emery 2007).

Given NC crows comparatively small social network size, it appears doubtful that social factors are responsible for the development of their remarkable cognitive skills and high degree of encephalization. However, it is possible that they have a relatively high number of intense relationships within their family. The core unit of NC crow sociality is the immediate family. This can include the breeding pair and offspring from the last two breeding seasons. Family members were present in 89% of all accompanied visits, and were the exclusive company in 82% of these visits. Moreover, pairs travel together year round and are accompanied by juveniles up to two years of age, except during the breeding season (Figures 2 and 3). After hatching, both parents contribute to raising the juveniles until they leave the parents. The two longest relationships observed lasted five years each, one of which is ongoing. I observed only one change of partnership, which happened when Pandora paired up with a new partner after her former mate was killed. I therefore assume that, like other corvids, NC crows generally mate for life. Their strong pair bond is consistent with Emery et al.’s (2007) idea that in birds the quality of the relationships between individuals is more relevant to the evolution of intelligence than the number of relationships.

Two main aspects distinguish NC crows from other corvids. First, parental care appears to be significantly longer than in most other species. Some other corvids, particularly those that breed communally like pinyon jays and American crows (*Corvus brachyrhynchos*), allow their juveniles to remain within the parental foraging area for extended periods after fledging (Caffrey 1992; Langen 1999; Clayton & Emery 2007). However, in most species juveniles disperse within a few months of fledging (Langen 1996; Russell 2000; Kaplan 2004). In contrast, juvenile crows on Maré lived in close association with their parents well into their second year of life. Parental feeding until the following breeding season was seen in all nine target families, and occasional feeding of 1-2 year old juveniles is not uncommon. The oldest offspring was 20 months old when last observed being fed. Emery et al. (2007) have suggested that a lifelong pair bond in a species with altricial offspring is cognitively demanding because parents have to cooperate until the offspring becomes independent. The extremely prolonged period of parental feeding in NC crows might therefore pose an additional cognitive load, as parents have to assess the demand of two (or more) differently developed juveniles (e.g. when to feed this year’s juvenile, and when to feed the previous year’s). Extended parental care could be advantageous for NC crows in several ways. At the end of their first year, juveniles have still not reached adult proficiency (in particular, adult speed) at complex foraging techniques such as pandanus tool manufacture and use (Holzhaider et al. 2010). Complex or time consuming foraging techniques also appear to result in extended parental care in other bird species. For example, co-operatively breeding Australian white-winged choughs

(*Corcorax melanorhamphos*) sift through patches of soil and leaf litter extremely thoroughly to catch arthropods (Rowling 1965). This foraging method appears to be so demanding that without the contribution of non-breeding helpers, parents are normally unable to provide sufficient food to successfully raise a clutch of juveniles (Boland et al. 1997). Accordingly, juvenile choughs take 4-8 months to become proficient enough for foraging independence and keep improving their foraging skill until they are about four years old (Heinsohn 1991). Similarly, royal terns (*Thalasseus elegans*) that forage for difficult-to-catch fish feed their juveniles until they are seven months old (Ashmole & Tovar 1968). In NC crows, the low frequency of parents feeding second-year offspring indicates that juveniles are nutritionally independent long before the parents stop feeding them. However, begging and subsequently getting fed might strengthen the juvenile-parent relationship so juveniles are allowed to continue living in close association with their parents. This might help juveniles to perfect their foraging skills in an environment of reduced intra-specific competition and predation threat. That juveniles delay dispersal to profit from a ‘safe haven’ provided by their parents has been suggested for other bird species such as the Siberian jay (*Perisoreus infaustus*) (Ekman & Griesser 2002). While older NC crow offspring do not appear to help their parents raise younger siblings directly, they might act as additional models for tool manufacture and use.

The second characteristic trait that distinguishes NC crows from other corvids is, of course, their tool use. Given NC crows’ comparatively small social network size, technical intelligence might provide an explanation for their considerable cognitive abilities and high degree of encephalization. Sterelny (2007) proposed a ‘social intelligence – ecological complexity hybrid’, arguing that social and technological competence became coupled in early hominines. Through niche construction (Odling-Smee et al. 2003; Sterelny 2003) early hominines changed their environment so it provided new challenges and opportunities to develop technology for future generations. NC crows' lifestyle is consistent with this idea because parents facilitate the acquisition of their juveniles' tool skills by strongly scaffolding their learning environment (Holzhaider et al. 2010). However, captive rooks, which do not use tools in the wild, have shown physical intelligence similar to that of tool using species (Emery & Clayton 2009; Bird & Emery 2009, 2010). Careful experimental work will be necessary to assess if and to what extent technical intelligence contributes to brain expansion and associated enhanced cognitive abilities.

The social organisation of NC crows on Maré appears to be potentially suitable for the evolution of the generational transmission of tool skills. NC crows make three different designs of pandanus tools that vary in complexity from uniformly wide or narrow tools to the more complex stepped tools (Hunt & Gray 2003). The three designs have a continuous and overlapping distribution with no obvious ecological correlates. Moreover, each design is characterised by a high degree of local standardization and the shape of a specific design at a site can remain stable for decades (Hunt & Gray 2003; G.R. Hunt unpublished data). The shape and design consistency suggests high fidelity social transmission of tool manufacture techniques over generations. Hunt and Gray (2003) proposed that the diversification of pandanus tools designs arose through a process of cumulative technological evolution.

Broadly speaking, social transmission within a population may either be vertical (from parent to offspring) or horizontal (between unrelated individuals) (Cavalli-Sforza & Feldman 1981; but see Boyd & Richerson 1985; Findlay et al. 1989; Allison 1992 for more detailed definitions). In particular, vertical transmission is considered to be crucial for the faithful transfer of improvements to established technologies (Sterelny 2006).

The social organisation of NC crows is likely to promote vertical transmission while minimising the opportunity for horizontal transmission. In general, close proximity between individuals increases the likelihood that one can observe details of the other's behaviour (Coussi-Corbel & Fragaszy 1995). Van Schaik et al. (1999) claim that strong mutual tolerance between individuals was a key factor in the evolution of technology among hominids, tied to a lifestyle involving food sharing and tool based processing of food. NC crows were highly tolerant towards family members with whom they readily shared feeding tables. Juveniles predominantly shared tables with their parents (Figure 2.5). Young juveniles are allowed to watch both tool use and tool manufacture from close proximity, use their parents' discarded tools, and are fed much of the food that parents extract (Holzhaider et al. 2010). Moreover, during the first 3–6 months post hatching juveniles spent up to 40% of their time at tables in the company of their parents. Juveniles therefore have ample opportunity to obtain tool skills vertically from their parents and any older siblings.

Nevertheless, juveniles also shared tables with non-family crows (Figure 2.5), and the target males appeared to be generally more tolerant of unrelated juveniles than of other adults (except their partner). Similarly, adult chimpanzees are highly tolerant of juveniles even if they are not their own offspring, which increases juveniles' opportunities to observe tool use by experienced individuals (Matsuzawa et al. 2001). However, I found that the opportunity for young crows to learn tool skills from their immediate family (vertical transmission) is likely to be much greater than from present non-family birds (horizontal transmission). Juveniles that shared a table with their parents often approached them very closely when they were engaged in tool use, sometimes even touching the tool as the parent was probing (Holzhaider et al. 2010). In contrast, I never observed a juvenile get this close to a non-family bird. Instead, they tended to keep their distance and often displayed submissively. Additionally, visits in which juveniles shared a table with a non-family adult were less frequent and tended to be much briefer than visits with family members. Horizontal transmission is therefore unlikely to play a major role in juveniles' learning of tool skills.

The proposed dominance of vertical versus horizontal transmission might also help to explain the co-existence of different pandanus tool designs at sites like Parc Rivière Bleue on Grande Terre (Hunt & Gray 2003). However, it is still unknown if individuals and/or families can make and use more than one pandanus tool design, or if they are restricted to one design only.

In summary, the lifestyle of NC crows fits well into that of other corvids. However, with a social network size of less than 20 individuals they are one of the less social species of the Corvidae. Their core unit is the immediate family, with whom they travel year round. Juveniles are tolerated and fed until well into their second year of life. NC crows' intense and long-lasting relationships with partners and juveniles is consistent with Emery's hypothesis that from a cognitive point of view, the quality of relationships is more important than the quantity, but insufficient to explain their impressive cognitive abilities. The long extended parental care and remarkable tool skills of NC crows are possible factors contributing to these abilities. The main direction of social transmission appears to be vertical, which is likely to support and enable the cumulative technological evolution of pandanus tool designs proposed by Hunt and Gray (2003).

3 Development of Tool Manufacture and Tool Use in wild New Caledonian Crows[2]

Abstract

New Caledonian crows have remarkably complex tool manufacture abilities. Here I document the ontogeny of pandanus tool manufacture in wild NC crows. My results show that the development of wide pandanus tool manufacture is a lengthy process comparable to the development of tool use in primates. Juveniles pass through four main stages of tool manufacture before they acquire adult-like proficiency. By 10 to 12 months of age most juveniles can manufacture tools with adult-like competency, but adult-like speed in manufacture and tool use is only reached in their second year. Whilst individual trial and error learning appears to play a major role in juveniles' development of pandanus tool skills, this development takes place in an environment scaffolded by parental birds. Juveniles stay close to their parents for their first year and have ample opportunity to observe parental tool manufacture and use. Parents influence the juveniles' early learning by leading them to pandanus trees where they provide discarded tools for early tool use. Exposure to parental tools might help juveniles form a mental template of functional tool design and thus facilitate the faithful transmission of local design traditions.

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[2] Based upon Holzhaider, J.C., Hunt, G.R. & Gray, R.D. (2010). The development of pandanus tool manufacture in wild New Caledonian crows. *Behaviour*. *147*, 553-586.

Introduction

Basic tool use occurs in many animals from insects to elephants, but complex tool skills are rare (Beck 1980). One famous example of complex tool skills is the manufacture of stick tools by wild chimpanzees to dip for ants and termites (Goodall 1968; McGrew 1974). Tool manufacture by chimpanzees in the Taï Forest usually involves detaching a stick from a tree, modifying its length, and then removing the bark and leaves (Boesch & Boesch 1990). Another example is nut cracking, which is considered to be one of the most complex tool behaviours in nonhuman primates because it involves the coordination of three objects (a nut, a hammer and an anvil) (Inoue-Nakamura & Matsuzawa 1997). Nut cracking has been observed in West African chimpanzee communities (Whiten et al. 1999, 2001), in tufted capuchin monkeys (*Cebus apella*) in Brazil (Fragaszy et al. 2004; Ottoni & Izar 2008) and in long-tailed macaques (*Macaca fascicularis aurea*) in South East Asia (Gumert et al. 2009). The variation in behavioural repertoires between populations of both chimpanzees and orangutans has been suggested to reflect different cultures maintained by social learning (e.g. Whiten et al. 1999, 2001; van Schaik et al. 2003).

The New Caledonian crow is the only bird species with complex tool skills (Hunt, 1996, 2000a, b; Hunt & Gray 2002, 2007). Besides crafting crochet-like hooked tools out of twigs (Hunt & Gray 2004b), NC crows manufacture three distinct tool designs from the barbed edges of pandanus leaves (Hunt & Gray 2003). These three designs vary in complexity from the simple uniformly wide and narrow designs to the more complex stepped, or tapered, design. The three designs have a continuous and overlapping geographical distribution on mainland Grand Terre, with no obvious ecological correlates. Each design is characterised by a high degree of local standardisation. The specific design made at a site can remain the same for decades, suggesting high fidelity transmission (Hunt

& Gray 2003, G.R. Hunt unpublished data). Hunt and Gray (2003) proposed that the diversification of pandanus tools arose through a process of cumulative technological evolution. However, little is known about the ontogeny of NC crows’ pandanus tool skills in the wild, or the extent to which various social learning mechanisms might be involved.

Social learning mechanisms can range in cognitive sophistication from low-level local and stimulus enhancement to high-level imitation. Laboratory experiments have shown that imitation is important in how human children learn tool skills (Want & Harris 2001, 2002; Call et al. 2005; Horner & Whiten 2005), while nonhuman apes appear more likely to emulate. That is, they copy the outcome of an action rather than its exact motor pattern (Tomasello et al. 1987; Nagell et al. 1993; Call & Tomasello 1994; Call et al. 2005; Horner & Whiten 2005; but see Whiten et al. 2009). It has been claimed that imitation is crucial for the faithful transmission of learnt behaviour and thus for the possibility of cumulative cultural evolution (Boyd & Richerson 1996; Tomasello 1999). Others challenge this view (Heyes 1993; Laland & Hoppitt 2003). For example, Heyes (1993) argues that the fidelity of transmission relies on insulating socially transmitted information from individual modification, rather than a particular learning process.

There is little evidence for true imitation in animals in the wild (Laland & Hoppitt 2003). Matsuzawa et al. (2001) propose a mechanism of ‘education by master – apprenticeship’ to describe the social learning process in wild chimpanzee communities. They suggest that in the first 4-5 years of a juvenile’s life adults (especially the mother) are highly tolerant and provide young chimpanzees with many opportunities to observe tool use, while the actual motor patterns are then learned individually. While not actively teaching, adults allow juveniles to watch actions from close proximity and to scrounge and interact with objects used in the process, thus facilitating the development of tool use

(Matsuzawa et al. 2001; Biro et al. 2006). Laboratory experiments confirm the importance of 'leftover' tools in the acquisition of tool using skills by naïve individuals (Hirata & Morimura 2000; Hirata & Celli 2003). This process can be interpreted as a case of epistemic niche construction, whereby organisms modify the learning environment of their offspring (Laland et al. 2000; Odling-Smee et al. 2003; Sterelny 2006). This niche construction might lead to the faithful transmission of behaviours in the absence of high-level learning mechanisms such as imitation (Reisman 2007).

Initial tool use in both humans and nonhuman primates is preceded by a long period of object exploration and learning. Infants in many primate species have a predisposition for certain manipulatory action patterns, such as banging a surface with a held object, that precede using objects as tools (human infants: Thelen & Smith 1994, Rochat 2001; capuching monkeys: Fragaszy & Adams-Curtis 1997; chimpanzees: Takeshita et al. 2005). Infants show all the elements of the behaviour in rudimentary form before assembling them correctly and in the right order to carry out proficient tool use (McGrew et al. 1979; Nishida & Hiraiwa 1982; Connolly & Dalgleish 1989; de Resende et al. 2008). The development of proficient tool use is also an extended process. For example, children require many months to successfully use a spoon to eat (Connolly & Dalgleish 1989), and even longer to accomplish more sophisticated tasks. Young chimpanzees at Bossou, as well as tufted capuchins in Brazil, take well over two years to learn to crack nuts (Inoue-Nakamura & Matsuzawa 1997; de Resende et al. 2008). By six years of age chimpanzees are still less efficient at ant-dipping than adults (Nishida & Hiraiwa 1982; Humle 2006).

Laboratory studies indicate that the development of tool use in NC crows follows a similar pattern to that described above for primates. Kenward et al. (2005, 2006) describe the ontogeny of tool-oriented behaviours in NC crows as a combination of inherited action patterns, social and individual learning and creative problem solving. The authors hand-raised four NC crows in artificial nests and provided them with sticks and food that could only be extracted with tools. As is the case with primates, food retrieval was preceded by precursor actions that resembled components of proficient tool use. However, compared to the long learning periods reported for young primates, all four hand-raised juveniles retrieved food relatively early at around 70 days of age. Two of the four juvenile crows were allowed to watch tool use by their human foster parents, which resulted in increased twig carrying and insertion rates. However, the tutoring did not influence the onset or proficiency of food extraction, indicating that social input might not be necessary to acquire proficiency in basic stick tool use. The same is true for other bird species that habitually use tools in the wild. Woodpecker finches showed similar pre-functional development of tool behaviour and acquired proficient stick tool use regardless of whether or not they had a tool-using model to learn from (Tebbich et al. 2001). Similarly, naïve Egyptian vultures (*Neophron percnopterus*) can develop the technique of throwing stones to break eggs without social input (Thouless et al. 1989). However, in the Kenward et al. (2006) study, the tutored crows also had a preference to handle objects that had been manipulated by the experimenters, indicating that stimulus enhancement might play a role in the acquisition of certain aspects of tool manufacture and use. Several weeks after developing stick tool use, the four crows were each presented with single, artificially mounted pandanus leaves. All the crows ripped at the leaves and removed strips of material. One three-month-old individual made a strip and used it as a probe on its first day of exposure to the leaf (Kenward et al. 2005). Kenward et al. concluded that basic tool manufacture and use can develop from a disposition to manipulate tool-like material to try and obtain out-of-reach food, without the need for social learning.

Hunt et al.'s (2007) observations of a hand-raised male NC crow at Parc Zoo-Forestier, Nouméa confirmed that basic tool skills can develop without social learning. This crow developed stick tool use and tore off pieces of provided pandanus leaves, but he did not use them to extract meat. Similarly, when four captive adult crows that lacked experience with pandanus leaves were given the opportunity to use and manufacture pandanus tools, only two of them used the provided tools and none manufactured tools. Hunt et al. (2007) proposed that a disposition for basic stick tool skills evolved early in the history of the NC crow's tool behaviour. With this disposition in place, crows then enhanced their stick tool skills and developed pandanus tool skills through individual and social learning. The fact that none of the pandanus tools manufactured by captive crows in Kenward et al.'s study resembled any of the three designs made in the wild is consistent with this hypothesis. Furthermore, the way these tools were manufactured did not resemble the distinct cutting and ripping techniques used by free-living adult crows to make pandanus tools (Hunt & Gray 2003, 2004a).

While research on hand-raised animals in the laboratory enables observations under controlled conditions, it does not necessarily model all processes that might lead to the development of complex behaviours in the wild. For example, the production of strips of pandanus leaf in the Kenward et al. (2005) study might be an artefact of impoverished living conditions in the laboratory. Adult crows held in our own outdoor aviary on the island of Maré sometimes also indiscriminately tear at pandanus leaves provided in their cages without using most of the leaf fragments as tools. Only a field study can reveal all the interactions between parents and offspring that might facilitate various forms of social learning. Investigating the development of tool manufacture and use in natural conditions is therefore crucial for exploring the mechanisms that actually underlie the transmission of complex tool skills. In this study I document the development of pandanus tool manufacture and use in wild NC crows. Over the course of two years I observed the tool development of six juvenile crows that visited feeding sites in their natural habitat. The study was carried out on the island of Maré, New Caledonia, where crows habitually manufacture wide pandanus tools and basic, non-hooked stick tools.

Methods

Study Site and Subjects

The study was carried out on the island of Maré, New Caledonia, about 5km inland from Wabao village. I observed crows at or close to feeding tables in the forest in most months in 2005 (January-May, July and October-December) and 2006 (January-May, August and October-December). One juvenile crow (Abel) was also subsequently observed in late 2008. NC crows breed on Maré during November and December and chicks have usually fledged by January.

I documented the behaviour of six juveniles that regularly visited the feeding tables. While other crows also occasionally visited the tables I only recorded data on target birds and their family members (parents and/or siblings, Table 3.1). Pandora's partner (and Primo's father; Family 1) was killed by a goshawk in November 2005, before Primo hatched. Pandora then paired with Abraxas (Family 2) around May 2005 and successfully raised Yor in 2006. Adam and Godot (Family 3) successfully raised two siblings, Cain and Abel, in the 2005/2006 breeding season. Klaus and Maui (Family 4) failed to raise chicks in 2003 and 2004, but successfully raised Bo in the 2005/2006 breeding season. Twiggy (Family 5) was observed only in December 2005 and his parents were unknown. All study animals (except for one female parent, Pandora), were banded with individually coloured leg bands. Some birds had previously participated in experimental work in 2003/2004 at feeding tables (Pandora) or in our on-site aviary (Abraxas).

Primo was placed in the aviary for one week in January 2006 to record tool manufacture and meat extraction in order to increase sample size in the 10-12 month age class. For Cain, data on tool preference, tool manufacture and meat extraction at 28 months of age was also obtained in the aviary in April 2008, after he participated in experiments unrelated to this study.

Procedure

Observations were made at feeding tables at various times throughout the day. Feeding tables were approximately 1m above the ground and made out of wood found in the vicinity. I positioned a fresh pandanus tree next to the table for pandanus tool manufacture, and usually a branch to encourage stick tool manufacture. On each table I placed a dead log in which I drilled vertical holes (6-7cm deep and 2.5cm in diameter). The holes were baited with pieces of meat that crows could only extract with tools. To create more natural feeding conditions, from April 2006 I usually also baited the pandanus tree at the table by pushing pieces of meat into crevices at the bases of the leaves. Over the course of the study I used eight feeding tables distributed in an area of ca. 0.4 km^2. Observations at tables were videotaped from hides set up 6-10m from tables. Video cameras were either handheld or operated automatically in conjunction with a motion detector (Wachit VMD-19M Video Motion Detector, Farco Technologies, New Zealand). During direct observation, the holes and the pandanus tree at the table were baited after each visit in which crows had extracted meat. At tables monitored automatically with a motion detector/camera, the holes and trees were baited several times a day.

Table 3.1. Details of target juveniles and their families.

	Crow	Status	Sex	Hatched	Fledged	Banding date
Family 1	Epi[x]	adult	m	-	-	23/09/2003
	Pandora	adult	f	-	-	unbanded
	Primo	juvenile	m	02/12/2004*	01/01/2005	30/12/2004
Family 2	Abraxas	adult	m	-	-	21/09/2003
	Pandora	adult	f	-	-	unbanded
	Yor	juvenile	m	13/11/2005*	14/12/2006	13/12/2006
Family 3	Adam	adult	m	-	-	23/07/2004
	Godot	adult	f	-	-	24/07/2004
	Cain	juvenile	m	06/11/2005*	06/12/2005*	14/02/2006
	Abel	juvenile	m	06/11/2005*	06/12/2005*	14/02/2006
Family 4	Klaus	adult	m	-	-	14/09/2003
	Maui	adult	f	-	-	14/09/2003
	Bo	juvenile	f	06/11/2005*	06/12/2005*	16/02/2006
Family 5	y/g	adult	m	-	-	-
	g/y	adult	f	-	-	-
	Twiggy	juvenile	m	Dec 2004[#]	Jan 2005[#]	04/08/2005

[x] died in late 2004 before Primo fledged. * Date estimated from observations at the nest..
[#] Date estimated from mouth colouring and behaviour at capture. m = male, f = female.
See band numbers in Table 2.1.

Table 3.2. Ethogram definitions of tool related behaviours (also see supplementary data CD, Videos 3.1 and 3.2).

Category	Behaviour	Measured	Description
Tool use	Wrong-angle probing*	d	Holding a twig and performing probing motions directed towards a hole. Because the twig is held at the wrong angle the hole is missed and no insertion takes place.
Tool use	Folding	d	Grasping a tool that is already inserted in a hole and bending or folding it in the hole.
Tool use	Defective probing	d	Probing with a tool that is inserted in a non-functional way (e.g. bent, both ends pointing upwards).
Tool use	Probing	d	Inserting tool into hole or crevice/inter-leaf space, followed by up and down movements with the head, holding the tool.
Tool manufacture	Technique 0	d, n	Apparently random, not sequential ripping at pandanus leaf that does not result in part of the leaf coming off.
Tool manufacture	Technique 1	d, n	Apparently random, not sequential ripping at pandanus leaf resulting in part of the leaf coming off and being used as a tool.
Tool manufacture	Technique 2	d, n	Coordinated sequence of cutting and ripping at a leaf edge. Because rips do not align, the crow cannot remove the tool from the leaf.
Tool manufacture	Technique 3	d, n	Coordinated sequence of cutting and ripping at a leaf edge. Because the second cut/rip is made proximal to the first, this results in a tool of adult-like shape but with the barbs pointing towards the working tip.
Tool manufacture	Technique 4	d, n	Adult-like tool manufacture. Coordinated sequence of cutting and ripping at a leaf edge resulting in a functional tool with the barbs pointing away from the working tip.

* Definition and description corresponds to that defined in Kenward et al. (2006). The tool use categories ‘wrong-angle probing’, ‘folding’ and ‘defective probing’ were combined into one category ‘faulty probing’ for analysis. d = duration of activity measured in seconds; n = frequency of behaviour or number of manufactured tools.

Data Analysis

Data extraction from video footage followed standard focal animal procedures (Altmann, 1974) and started whenever a focal juvenile landed on a feeding table. By observing video footage of one juvenile (Primo) I defined nine tool-related behaviours to describe the development of proficiency in pandanus tool manufacture and use (Table 3.2 and supplementary Data CD, Videos 3.1 and 3.2). Four of these nine behaviours describe tool use, and the remaining five tool manufacture (techniques 0-4). The manufacture techniques range from unsuccessful, random-like ripping of leaves (Technique 0) to adult-like manufacture (Technique 4). For each visit by a target crow to a feeding table I recorded: (1) visit duration, (2) the family members that shared the table, (3) the number of tools manufactured and used, (4) the duration of each tool manufacture from the moment a crow touched the leaf with the bill to the removal of the tool from the leaf, (5) the amount of time probing for meat (probing was recorded only when a crow was actively using a tool in a hole), (6) the occurrence of tool-related behaviours according to Table 3.2, (7) whether a juvenile watched parental tool manufacture and meat extraction (see below for more details), and (8) parental feeding of a juvenile.

A juvenile was recorded as watching its parent only when the following four criteria were met: (1) the distance to the parent was less than ca. 1 m, (2) the juvenile was either side-on to the parent or facing it, (3) the juvenile was not obviously engaged in another activity (e.g. eating or using a tool), and (4) the line of vision between juvenile and parent was not obstructed.

I measured the development of proficiency in pandanus tool manufacture over time in various ways. First, I separated the developmental period into four post-hatching age classes: 2-3 months, 4-6 months, 7-9 months and 10-12 months. I only began collecting data at the end of the second month post-hatching because juveniles only visited the feeding tables from that time onwards. I calculated the frequency that individuals in each age class used each of the five manufacture techniques (Table 3.2). To measure probing efficiency I first calculated the ratio of faulty probing time (first three tool use categories in Table 3.2 combined) to total probing time (whether successful or not) for each bird in each age class, then the mean ratio across individuals in the age classes. For meat extraction times I first calculated the mean extraction time per visit to a feeding table (total amount of successful probing time (s) divided by the number of extractions). I then calculated the mean extraction time across individuals in each age class. To determine the amount of unrewarded probing, I calculated the time spent in unsuccessful probing events in relation to total probing time in each age class.

Data were analysed using non-parametric statistics because they did not conform to assumptions for normality. Spearman's Rho was used to correlate age with the development of different measures of tool manufacture and use. To calculate correlations I only used juveniles that provided data in at least three different age classes and developed a preference for pandanus tools (Primo, Yor and Cain). Data for these birds was combined. Yor rarely extracted meat from the provided logs, therefore I could only analyze the tool use of Primo and Cain. All correlations were one-tailed. I used chi-square tests to compare the following behaviour between individual adult and juvenile pairings: the frequency of tool manufacture techniques, unrewarded probing and tool manufacture variants. To determine whether a crow had a dominant tool manufacture variant I tested the frequency of the most used variant against the combined frequencies of the two variants the crow used least. Binomial tests were used to identify individual preferences for either stick or pandanus tools. The chi-square and binomial tests were two-tailed. Mann-Whitney *U*-tests were used to compare extraction times and the duration of tool manufacture between individual adult and juvenile pairings. The alpha level was 0.05 for all tests.

Results

During ca. 1790 hours of direct observation and 2000 hours of observation with motion detector units I video-taped ca. 30 hours of juvenile crow behaviour. I recorded 716 visits to feeding tables by the six target juveniles. Their visits lasted on average 4.1min (range = 4s to 22.1min). I recorded the manufacture of 615 pandanus tools by the six juveniles and 421 tools by their parents. I observed the juveniles extract 521 pieces of meat with pandanus tools from holes and pandanus trees and their parents extract 469 pieces of meat.

Opportunity to Watch Parental Tool Manufacture and Use

Four juveniles (Primo, Yor, Cain and Abel) regularly visited feeding tables with at least one pandanus tool-using parent, sharing a table with the parent for 30 to 40% of the visiting time up to six months of age (Figure 3.1). The parents manufactured pandanus tools at an average rate of 0.01 tools per minute of visit time. The proportion of time spent with their parents declined with age (Spearman's $r = -0.73$, $N = 12$, $p < 0.004$). In each age class, juveniles watched parents extract meat from holes and trees more frequently than they watched pandanus tool manufacture. This difference was only non-significant at 7-9 months of age (Figure 3.2, 2-3 months: $\chi^2 = 7.7$, df = 1, $p = 0.006$; 4-6 months: $\chi^2 = 104.2$, df = 1, $p < 0.001$; 7-9 months: $\chi^2 = 3.1$, df = 1, $p = 0.08$, 10-12 months: $\chi^2 = 5.0$, df = 1, $p = 0.03$). Juveniles often approached a parent very closely when it was extracting meat with a tool, sometimes looking into the hole that the parent was extracting meat from and even touching the tool that the parent was using. This was not the case with juveniles watching tool manufacture, which was mostly from some distance away.

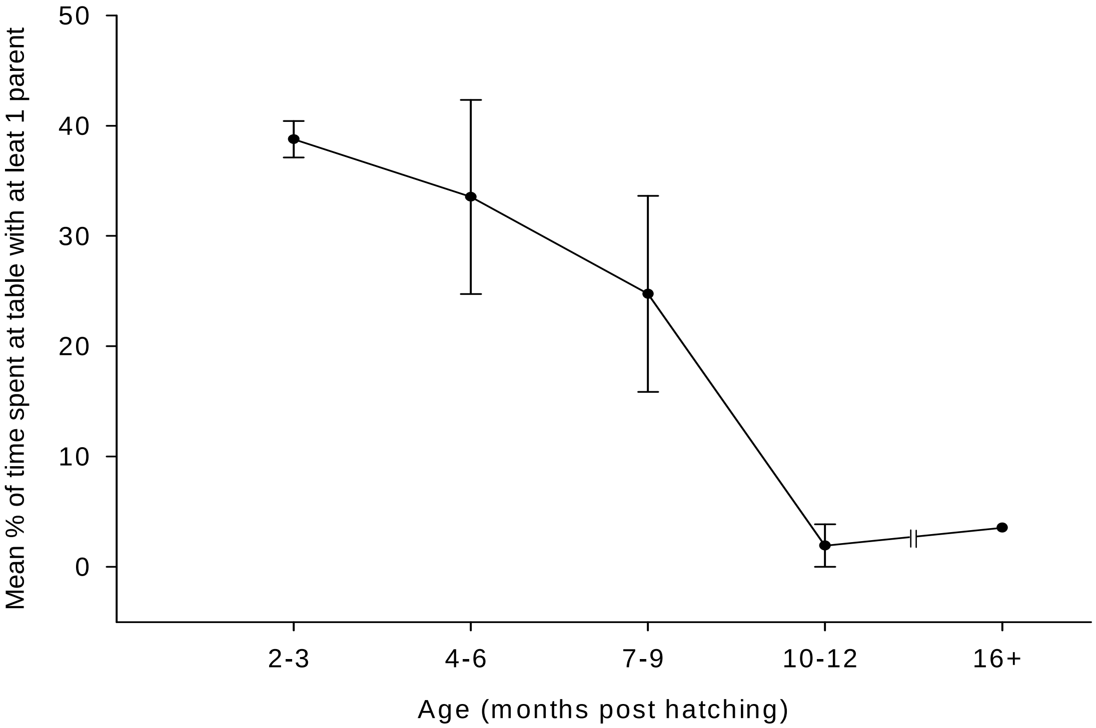

Figure 3.1. Mean percentage of time spent with parent(s) at feeding table. Error bars represent 1 SE.

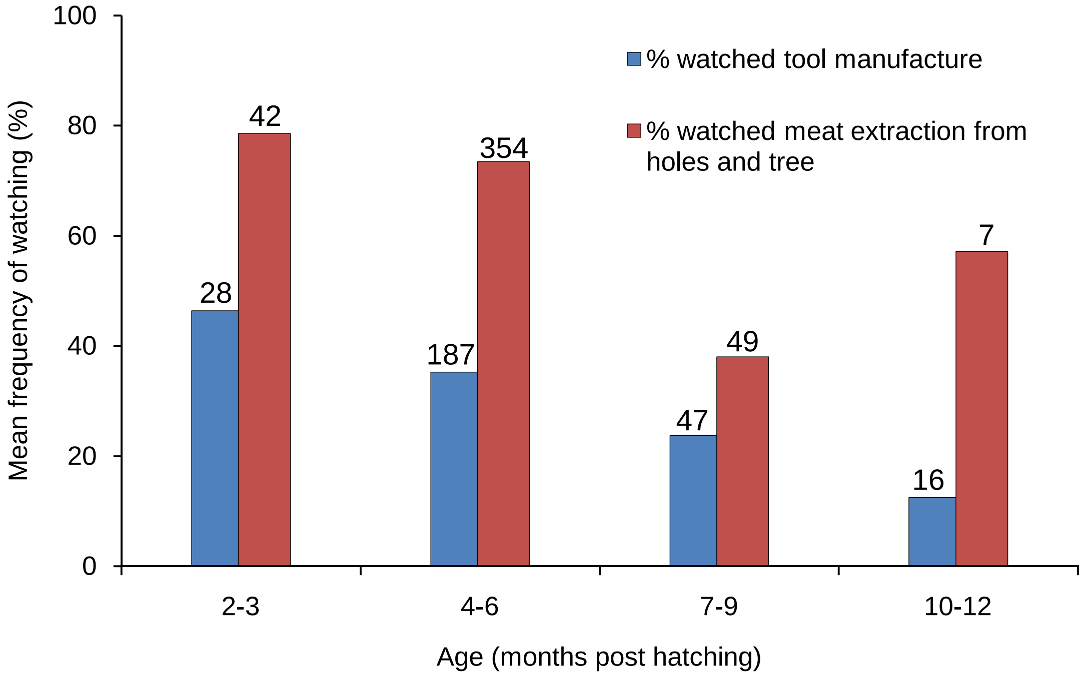

Figure 3.2. Juveniles watching tool manufacture and meat extraction. The numbers on top of the bars represent the total numbers of parental tool manufactures and meat extractions when a juvenile was present. Only Cain contributed to the 10-12 months age class.

Development of Pandanus Tool Manufacture

Development of tool manufacture techniques

Pandanus tool manufacture developed similarly in Primo, Yor and Cain (Figure 3.3). Techniques 0 and 1 (uncoordinated ripping at pandanus leaves that sometimes resulted in a tool, see video 3.2 for tool manufacture techniques) were used mostly up to six months of age. The relative frequency of this behaviour declined with age (data combined for Primo, Yor and Cain, Technique 0: Spearman's $r = -0.95$, $N = 10$, $p < 0.001$, Technique 1: Spearman's $r = -0.55$, $N = 10$, $p = 0.049$). From about four months of age juveniles employed more coordinated sequences of ripping and cutting at leaf edges. Because these rips did not align (Technique 2) or were performed in the wrong order (Technique 3), the tools either could not be removed from the leaf or were oriented with the barbs pointing downwards and therefore were not immediately functional. The frequency of Techniques 2 and 3 was low and constant across age classes after 3 months of age. Adult-like tool manufacture (Technique 4: coordinated sequence of cutting and ripping that produced a correctly oriented, functional tool) appeared first at 4-6 months of age, and its frequency increased over time (data combined for Primo, Yor and Cain: Spearman's $r = -0.77$, $N = 10$, $p < 0.005$).

However, at 10-12 months of age the relative frequency of adult-like tool manufacture was still significantly lower than that of their respective parents for two of the three juveniles (Figure 3.3; Primo: $\chi^2 = 21.9$, df = 1, $p < 0.001$; Cain: $\chi^2 = 22.9$, df = 1, $p < 0.001$). Yor was making pandanus tools in adult-like fashion and frequency at 7-9 months of age ($\chi^2 = 0.1$, df = 1, $p = 0.74$). At 16 and 28 months of age Primo and Cain, respectively, had adult-like frequencies of manufacture techniques (Primo: $\chi^2 = 3.6$, df = 1, $p = 0.09$; Cain: $\chi^2 = 0.4$, df = 1, $p = 0.54$).

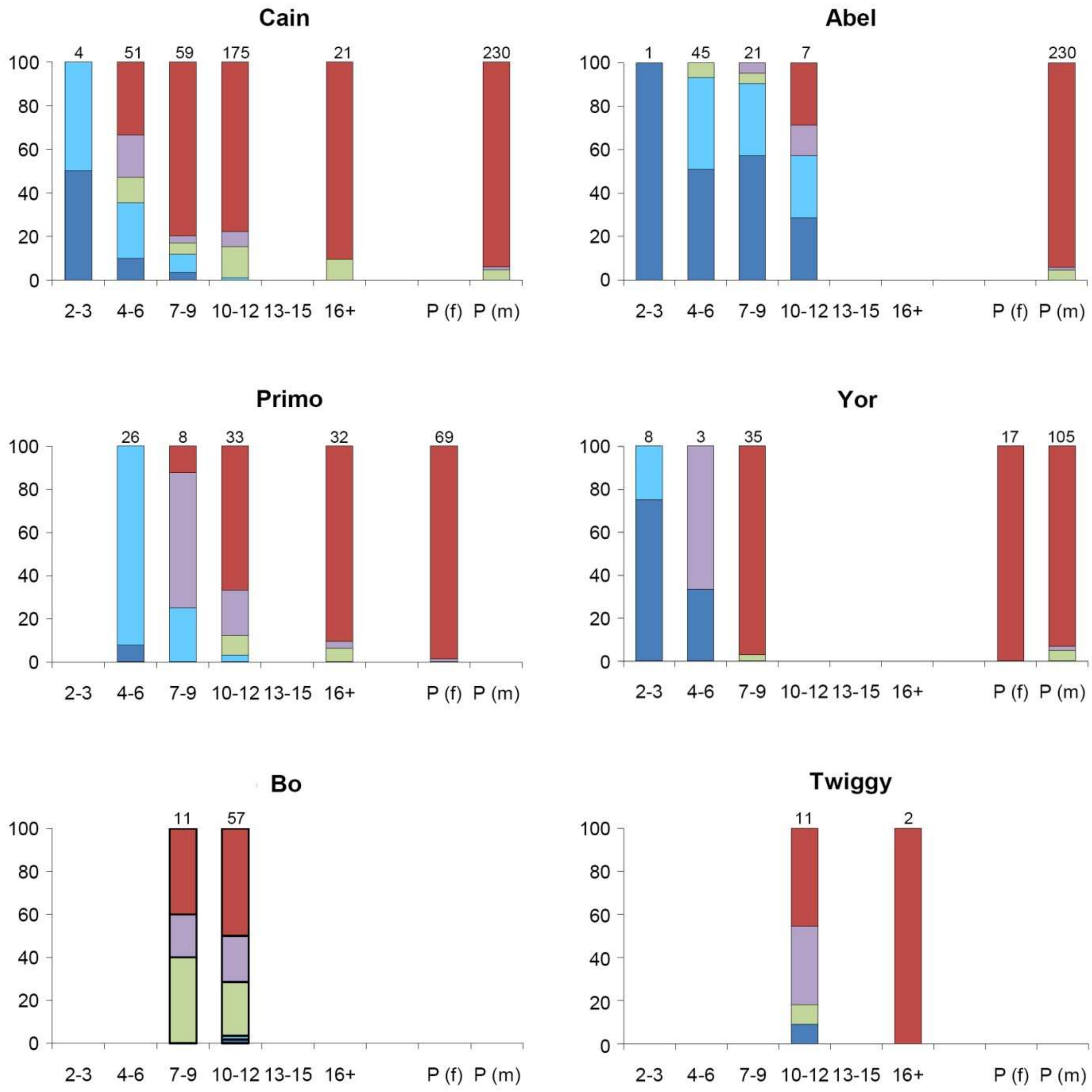

Figure 3.3. Individual development of pandanus tool manufacture techniques.

🟦 Technique 0 (random rips, no tool removed)

🟦 Technique 1 (random rips, tool removed)

🟩 Technique 2 (coordinated, non-aligning rips, no tool removed)

🟪 Technique 3 (coordinated rips in wrong order, barbs towards working tip)

🟥 Technique 4 (adult-like tool manufacture)

P = Parent; f = female; m = male. X-axis: Age (months post hatching). Y-axis: Frequency of manufacture technique (%). The numbers on top of the bars represent the total number of tools manufactured in each age class.

I observed no parental tool manufacture for juveniles Bo and Twiggy. There was insufficient data to statistically correlate age with manufacture techniques for Bo and Twiggy, but the relative frequencies of techniques used by them fit the pattern shown by Primo, Yor and Cain (Figure 3.3). Abel’s performance differed considerably from the other juveniles in that adult-like tool manufacture only appeared twice at 12 months of age. Because Abel is the only juvenile that preferred to pick up stick tools rather than manufacture pandanus tools (Table 3.3), I excluded him from all analyses concerning pandanus tool manufacture and use.

The shape of pandanus tools generally reflect the technique that they were manufactured with (Figure 3.4). Technique 1 tools do not closely resemble the shape of a classic wide pandanus tool (uniformly wide with barbs along one edge). Technique 0 and 2 tools cannot be removed from the leaf and remain on the pandanus tree. Technique 3 tools were adult-like in shape, but not immediately functional because the barbs point downwards. Technique 4 tools cannot be distinguished from adult tools.

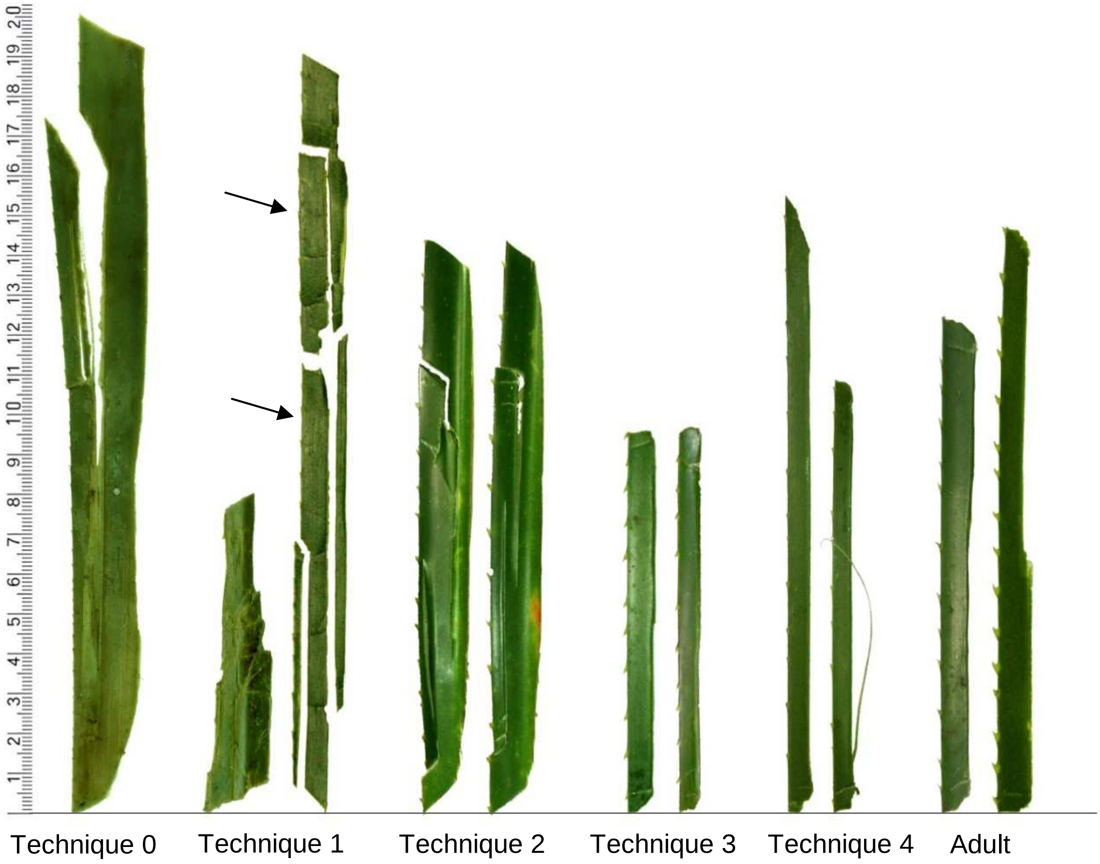

Figure 3.4. Examples of tools manufactured with Techniques 0-4 compared with adult tools. Techniques 0 and 2 do not result in a tool being removed from the leaf. I therefore show the section of the leaf where the tool manufacture had been attempted. The right hand tool of Technique 1 is the result of multiple uncoordinated ripping at the same leaf; only the two pieces indicated by arrows were used to probe in a hole. Techniques 3 and 4 produce adult-like tools, but the tools in Technique 3 are removed from the leaf in the wrong orientation. The stringy edge of the right hand tool for Technique 4 is caused by rips that do not align perfectly. All tools are oriented with the working end pointing downwards. The scale indicates cm.

Duration of tool manufacture

Manufacture Technique 4 appears to indicate adult-like technical proficiency in producing wide tools. However, juveniles using Technique 4 took longer to manufacture tools than their parents, and at 10-12 months still had not reached the speed of their respective parent's manufacture (Figure 3.5; Primo/Pandora: $U = 204.5$, $N_1 = 22$, $N_2 = 68$, $p < 0.001$; Yor/Pandora + Abraxas: $U = 566$, $N_1 = 37$, $N_2 = 93$, $p < 0.001$; Cain/Adam: $U = 6929$, $N_1 = 136$, $N_2 = 160$, $p < 0.001$). The duration of juveniles' tool manufacture is negatively correlated with age, indicating an increase in manufacture speed over time (Spearman's $r = -0.13$, $N = 260$, $p = 0.016$). By 16 months of age Primo had reached the manufacture speed of his mother ($U = 827$, $N_1 = 31$, $N_2 = 68$, $p = 0.08$), while Cain at 28 months of age still took significantly longer than his father to manufacture wide pandanus tools ($U = 389$, $N_1 = 12$, $N_2 = 160$, $p < 0.001$).

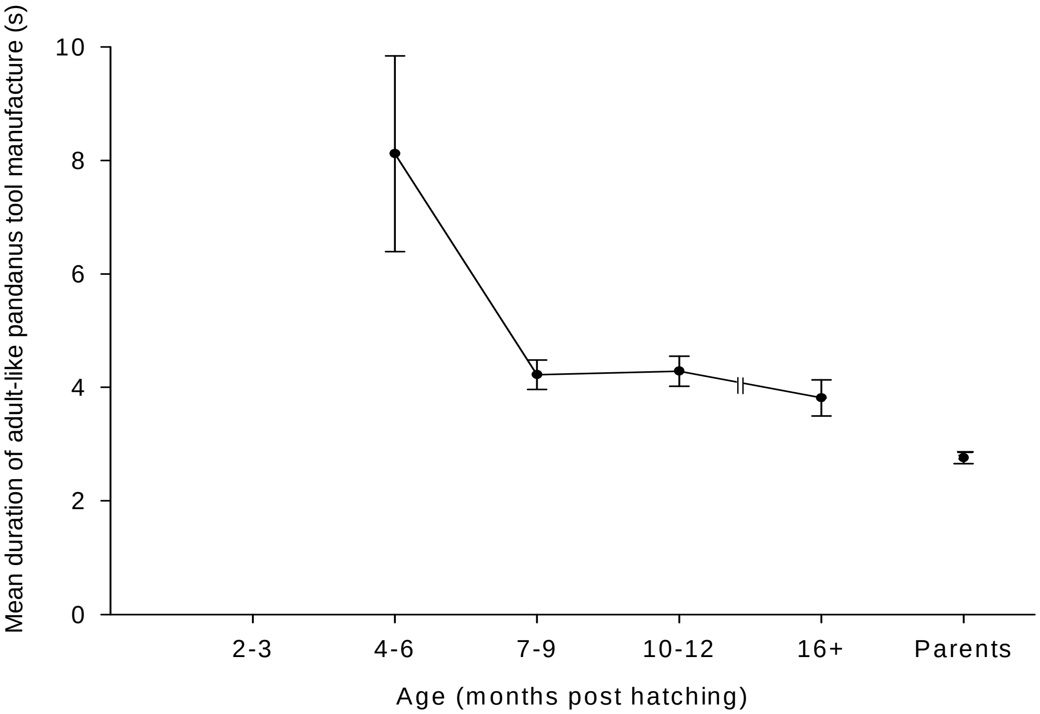

Figure 3.5. Duration of adult-like tool manufacture. Error bars represent 1 SE.

Variants of tool manufacture

Close examination of manufacture techniques revealed three different variants of wide tool manufacture (Figure 3.6, Video 3.3). In Variant A (cut-rip and cut-rip), two cut-rip sequences converge about half way along the tool. In variant B (cut-rip and cut), the first cut is followed by a long rip (action 1). The tool is then removed from the main leaf with only a cut (action 2). In variant C (cut and cut-rip) the actions in variant B are reversed: only a cut (action 1) is made initially, then the tool is removed by a cut-rip sequence (action 2). All variants may also occur when birds use manufacture techniques 2 (rips do not align, therefore the tool cannot be removed from the leaf) and 3 (second cut/rip starts proximal to the first cut/rip, therefore the tool is removed with the barbs pointing towards the working tip).

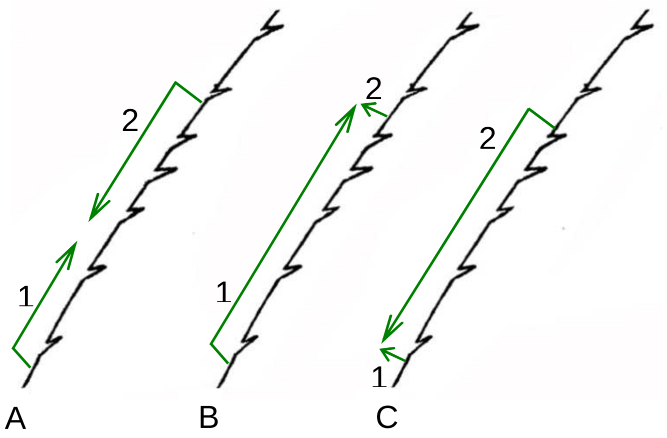

Figure 3.6. Variants of tool manufacture. Variant A: two cut-rip sequences converge about half way along the tool. Variant B: A cut-rip (1) is followed by a cut (2). Variant C: A cut (1) is followed by a cut-rip (2).

Figure 3.7 shows the frequencies that families 1-3 used these variants (juveniles in these families often visited tables with at least one parent). Abraxas was the only bird in these families that did not have a significant preference for a particular variant. While Pandora clearly preferred variant B ($\chi^2 = 27.6$, df = 1, $p < 0.001$), both her juveniles (Primo and Yor) predominantly manufactured tools by variant A (Primo: $\chi^2 = 24$, df = 1, $p < 0.001$; Yor $\chi^2 = 7.1$, df = 1, $p < 0.011$). Yor and Primo used variant A significantly more often than any individual in this family (all $\chi^2 > 10.2$, all df = 1, all $p < 0.002$). In Family 3, Adam preferred to use variant A while his juvenile Cain was the only crow with a preference for variant C (Adam: $\chi^2 = 34.8$, df = 1, $p < 0.001$; Cain: $\chi^2 = 7.1$, df = 1, $p = 0.009$). However, both Caine and Adam used variant C significantly more often than any crow in Pandora's families (chi-square tests for Cain and Adam vs. each member of Pandora's family: all $\chi^2 > 9.85$, all df = 1, all $p < 0.002$).

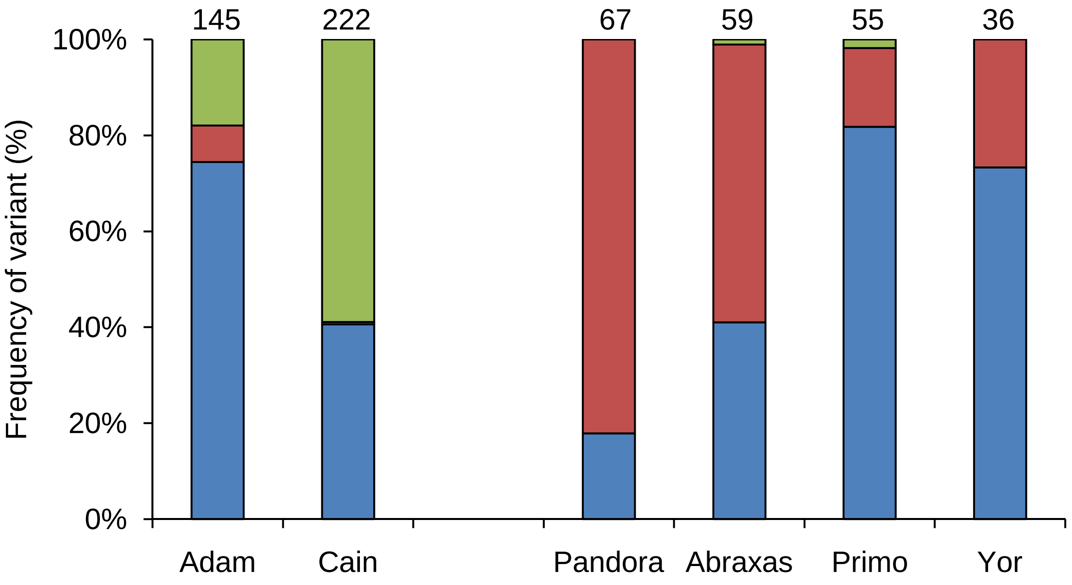

Figure 3.7. Frequency of tool manufacture variants. Sample sizes are on top of bars.

🟦 Variant A 🟥 Variant B 🟩 Variant C

Starting pandanus tool manufacture at damaged leaf edge

The process of pandanus tool manufacture means that the missing section of leaf edge resulting from manufacture is an exact template, or counterpart, of the shape of the removed tool (Hunt 2000a). While adult crows usually start tool manufacture at an intact leaf edge, juveniles frequently began tool manufacture at counterparts or other damaged parts of a leaf such as unfinished tools or broken edges (Figure 3.8). The proportion of tool manufactures starting at intact leaves increased with age. At 10-12 months of age Cain rarely began tool manufacture where there was leaf damage, while at 16 months of age Primo still did so more than his mother Pandora (Cain: 3.6%, N = 169, Adam: 0.9%, N = 225, χ^2 = 3.4, df = 1, p = 0.06; Primo: 13.9%, N = 63, Pandora: 0%, N = 17, χ^2 = 6.9, df = 1, p = 0.009).

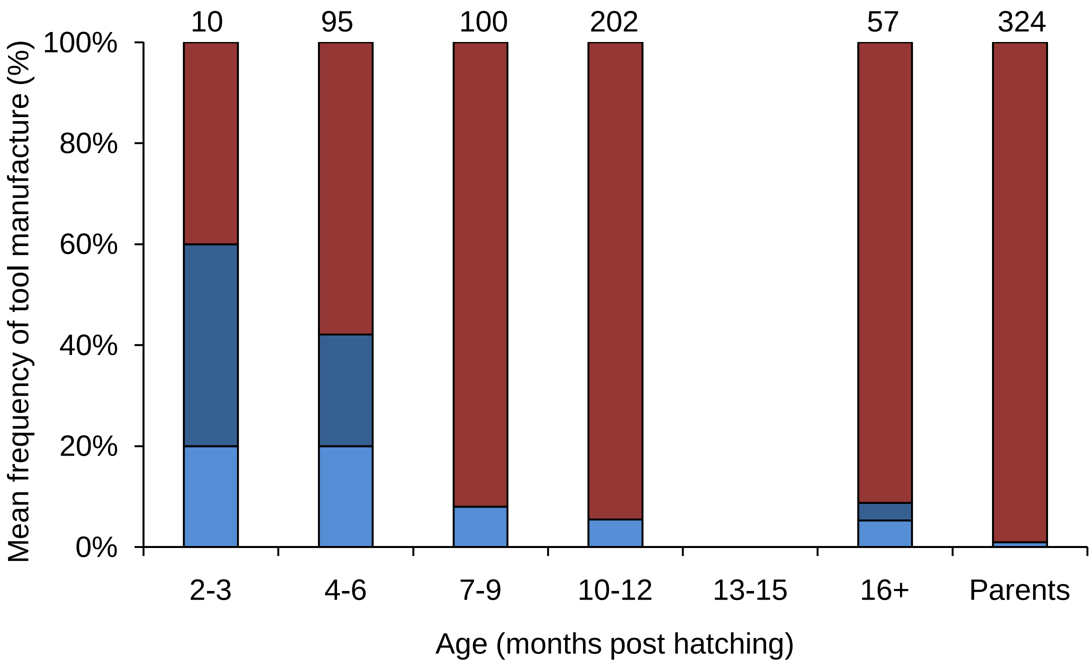

Figure 3.8. Average frequency of pandanus tool manufacture starting at counterparts or other damaged parts of the leaf. Numbers on top of bars represent the total number of tool manufactures per age class. 🟦 at CP 🟦 at other damaged parts of the leaf 🟥 at intact leaf

Development of Tool Preference

Adult NC crows at our study site usually have a distinct preference to manufacture and use either stick tools or pandanus tools (Hunt & Gray, 2007). All juveniles had at least one parent that preferred pandanus tools. Juveniles tended to use and/or manufacture both stick tools and pandanus tools during the first six months post hatching. By 10-12 months of age all juveniles except Abel had developed a preference for pandanus tool manufacture (Table 3.3).

Table 3.3. Preference for use and manufacture of pandanus or stick tools at tables in each age class.

Crow	**tool**	**2-3**	**4-6**	**7-9**	**10-12**	**16+**	**Parent (m)**	**Parent (f)**
Primo	p	11/1*	22/24	1/8	2/33*	6/34*		0/69*
	s	0/3	17/13	1/3	3/0	0/0		0/0
Yor	p	6/8*	4/3	21/39*			0/105*	0/17*
	s	1/0	2/0	0/0			19/0	0/0
Cain	p	1/4	50/51*	9/59*	8/175*	16/21*	0/230*	?
	s	1/0	2/2	2/0	5/0	8/0	0/0	?
Abel	p	4/1	76/45*	34/21	31/7	2/3	0/230*	?
	s	1/0	48/11	42/6	90/3*	14/1*	0/0	?
Bo	p			1/11*	2/57*		0/0	(22/22*)
	s			0/0	9/0		42/8*	(0/0)
Twiggy	p				0/11*	0/2	?	?
	s				0/0	0/0	?	?

The first number indicates tools picked up on, or brought to, the table for use, and the second number indicates tools manufactured at the table. p = pandanus, s = stick. * indicates a significant preference for either stick or pandanus tools (picked up + manufactured tools, binomial test, $p < 0.05$). For Bo’s mother, tool preference had been established in 2004. Data for Abel at over 16 months is based on observations in 2008 when he was between 2 and 3 years old.

When using tools they had not manufactured themselves, the birds discriminated less between a stick and a pandanus tool. However, at 10-12 months of age the juveniles’ use of tools that they had not made was minimal. The tool preferences appeared to continue into adulthood: Primo and Cain still preferred pandanus tools at 16 and 28 months of age, respectively. Observations of Abel at ca. 3 years of age suggested that he still preferred stick tools to pandanus tools (Table 3.3).

Development of Pandanus Tool Use

Origin of pandanus tools used at feeding tables

Up to six months of age the juveniles mainly used tools that had been left at the table by other crows (Figure 3.9). Many of these tools (38 of 94) had been used by a parent immediately before the juvenile picked it up. The frequency of use of parents' tools might be higher than I documented because some of the tools of unknown origin that juveniles picked up may have also been made by a parent. From seven months of age onwards, juveniles predominantly used tools they had manufactured themselves (Spearman's $r = 0.93$, $N = 11$, $p < 0.001$).

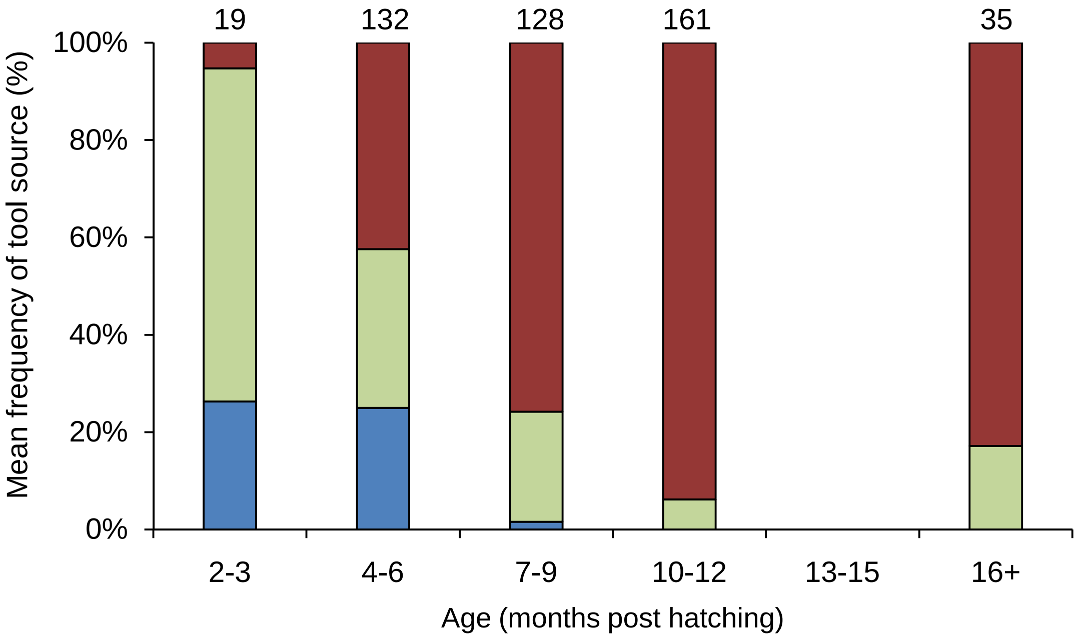

Figure 3.9. Origin of pandanus tools used at tables. Numbers on top of bars represent the total number of tools per age class. 🟦 parent's tools 🟩 other tools 🟥 own tools

Development of proficient pandanus tool probing

Juveniles made three main mistakes when trying to extract meat from a hole with a pandanus tool: (1) wrong-angle probing, (2) folding a tool in a hole, and (3) defective probing (Table 3.2). I combined these three behaviours into one category, 'faulty probing', because wrong-angle probing and folding rarely occurred. Faulty probing declined with age (Figure 3.10, Spearman's $r = -0.87$, $N = 7$, $p < 0.05$); after six months of age it accounted for less than 2 % of the total probing time.

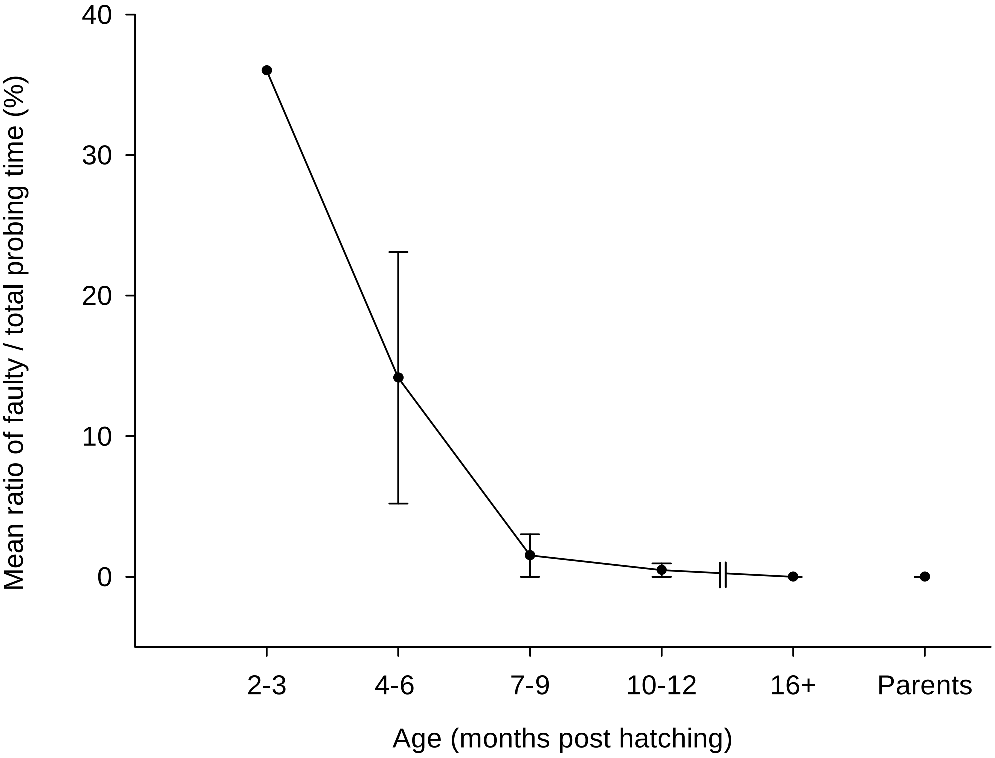

Figure 3.10. Mean ratio of faulty probing time to total probing time. Only Primo contributed to the 2-3 months age class. Error bars represent 1 SE.

Rewarded probing

The time it took juveniles to successfully extract pieces of meat from holes declined over time (Figure 3.11; Spearman's $r = -0.43$, $N = 69$, $p < 0.001$). However, at 10-12 months of age both Primo (*Mdn* = 27.0) and Cain (*Mdn* = 13.6) still took significantly longer to extract meat than their respective parents (Primo/Pandora (*Mdn* = 6.0): $U = 71.5$, $N_1 = 11$, $N_2 = 44$, $z = -3.59$, $p < 0.001$, $r = -0.48$; Cain/Adam (*Mdn* = 7.1): $U = 429$, $N_1 = 40$, $N_2 = 39$, $p < 0.001$). Primo's (*Mdn* = 16.8) and Cain's (*Mdn* = 11.0) extraction times did not differ significantly from their parents' at 16 and 28 months, respectively (Primo/Pandora: $U = 95.5$, $N_1 = 5$, $N_2 = 44$, $p = 0.63$; Cain/Adam: $U = 364.5$, $N_1 = 23$, $N_2 = 39$, $p = 0.11$).

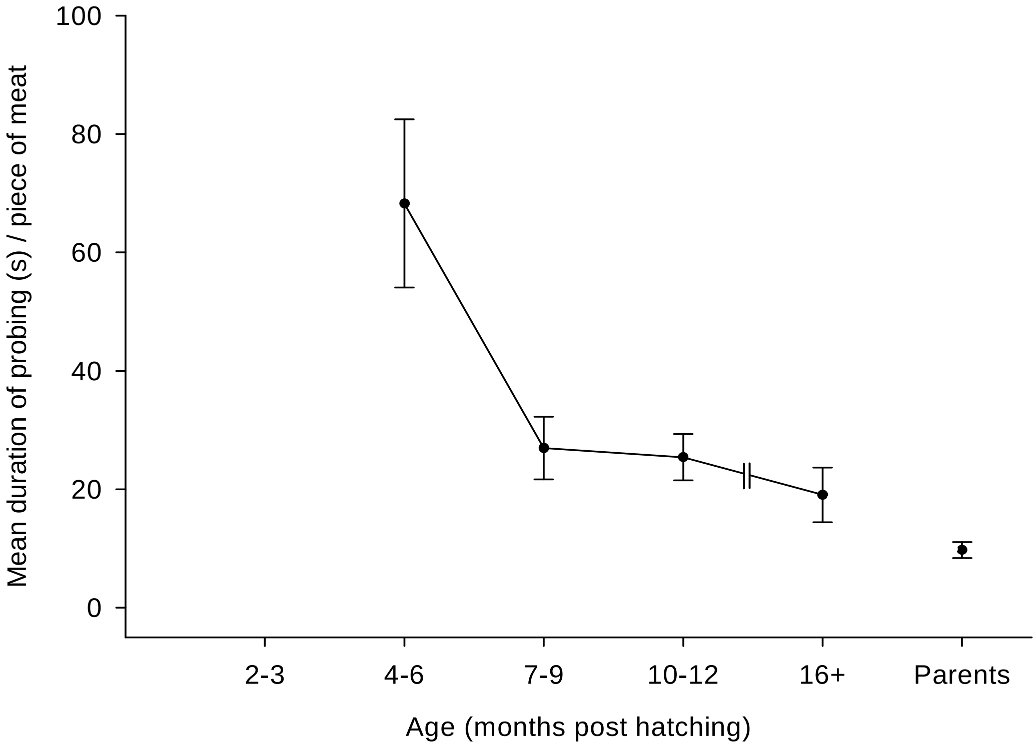

Figure 3.11. Mean duration of rewarded probing per piece of extracted meat from the holes in logs. Both Primo and Cain had reached adult-like speed at meat extraction at 18 and 28 months, respectively. Error bars represent 1 SE.

Unrewarded probing

A characteristic of juveniles' pandanus tool use was their persistence in probing without being rewarded. Up to six months of age they spent over 50% of total probing time in unrewarded probing episodes (Figure 3.12). Although this ratio declined with age, juveniles still spent more time in unrewarded probing episodes at over 16 months of age than their respective parents (Primo over 16 months compared to Pandora: $\chi^2 = 48.9$, df = 1, $p < 0.001$; Cain at 28 months compared to Adam: $\chi^2 = 206.6$, df = 1, $p < 0.001$).

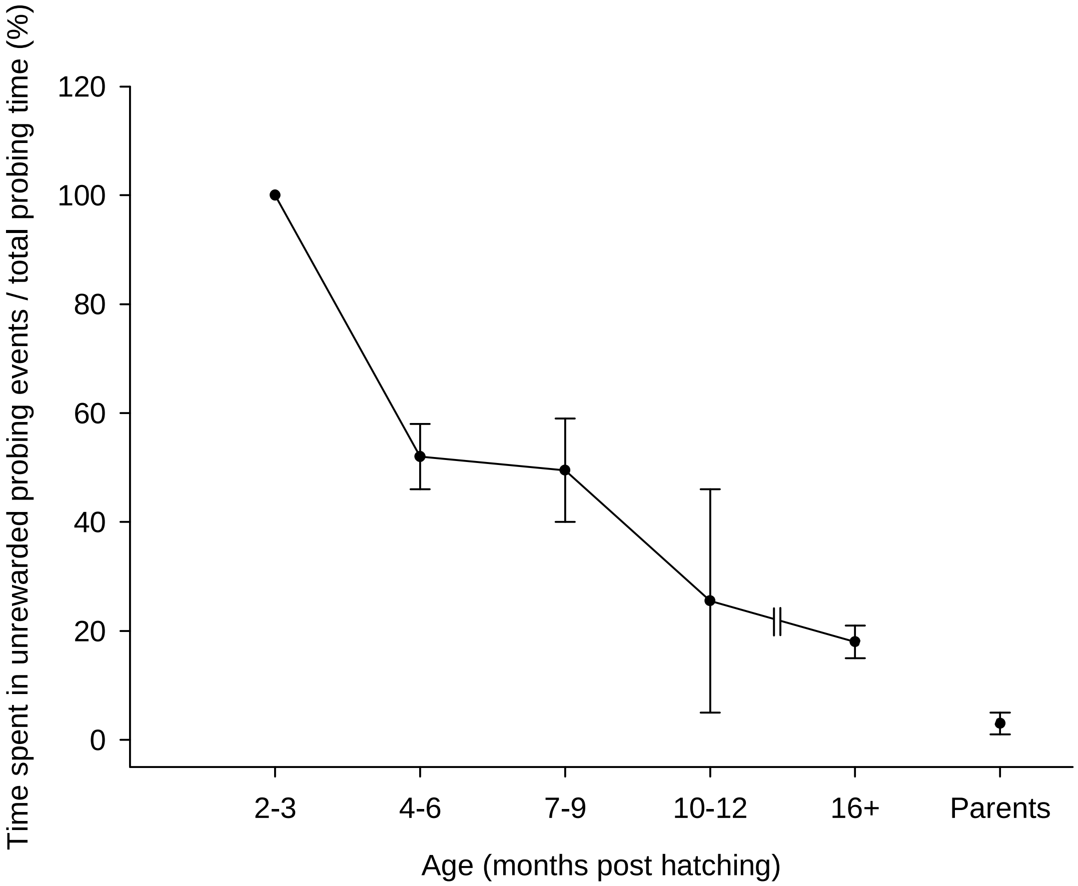

Figure 3.12. Mean ratio of unrewarded probing time to total probing time. Only Primo contributed to the 2-3 months age class. Error bars represent 1 SE.

Parental Feeding

Although juveniles up to six months of age spend a considerable amount of time on unsuccessful probing episodes (Figure 3.12), they were frequently fed meat that their parents extracted (Table 3.4). For example, when Cain was 4-6 months of age his father Adam, extracted 192 pieces of meat at feeding tables and subsequently fed meat to Cain 103 times. Because a juvenile may be fed more than one piece of meat at a time Cain may have received more than 103 pieces.

Table 3.4. Parental feeding at tables in each age class.

Crow	**2-3**	**4-6**	**7-9**	**10-12**	**16+**
Primo	20/6	63/35	0/0	0/0	0/0
Yor	19/3	10/2	25/2		
Cain	2/1	192/103	25/0	4/0	
Abel	3/0	222/79	21/5	2/0	
Bo	14/2	6/2	5/0	11/0	

The first number gives the total number of meat pieces extracted by parents from holes and pandanus trees in the presence of the juvenile. The second number gives the number of times parents subsequently fed the juvenile.

Discussion

The results of my field study contrast with the rapid development of basic tool use observed in four hand-raised crows by Kenward et al. (2005; 2006). I found that the development of even the most basic form of pandanus tool manufacture (i.e. wide tools) is an extended process where juveniles reach adult proficiency only after a year or longer post-hatching. My results are consistent, though, with the lengthy ontogeny of tool use in primates under natural conditions. For example, before human children master the complex task of using a spoon they perform repetitive actions like putting the spoon in the dish and removing it again (Connolly & Dalgleish 1989). This is followed by more complicated action sequences (e.g. putting the spoon in the dish then in the mouth). Later on they incorporate functional actions (filling the spoon with food and eating) and eventually they include correction loops like checking if food is on the spoon before they put it in the mouth. Both chimpanzees and capuchins start learning about nut cracking by exploring surfaces, carrying out simple pounding actions of both nuts and stones and placing objects on surfaces (Visalberghi 1987; Inoue-Nakamura & Matsuzawa 1997; de Resende et al. 2008). Such behaviour occurs before they correctly assemble all the physical elements of nut cracking and begin to open nuts successfully after two to three years of practice. Chimpanzees do not reach adult-like proficiency until they are nine to ten years old (Matsuzawa 1994). Captive hand raised NC crows had predictable precursor actions that resembled aspects of experienced tool use but were not directly functional, such as rubbing a stick against a substrate and wrong-angle probing. These precursor actions preceded successful food extraction and reached their maximum frequency at around eight weeks of age (Kenward et al. 2006). The reluctance of very young crows to come down to feeding tables meant that my earliest observations began only when the juveniles were eight weeks of age. This may explain why I rarely observed the precursor actions described by Kenward et al. (2006). However, I did find that juveniles went through four distinct subsequent stages in the development of proficient wide pandanus tool manufacture (Figures 3.3 and 3.4). At stage I the first attempts to manufacture pandanus tools consisted of uncoordinated ripping of Pandanus leaves, which often failed to produce a tool. If crows successfully removed the tool it often did not resemble the classic shape of an adult-made wide tool, or lacked barbs because it was removed at unsuitable locations for manufacture. At stage II the crows only gradually produced adult-like wide tools with a well-coordinated sequence of cutting and ripping actions. Their use of adult-like cutting and ripping actions still did not always result in the removal of a functional tool from the leaf because they made errors in the position of a cut or a rip. Adults generally position the second cut/rip action distal to the first one, and both cuts have the same depth. They can therefore remove the tool easily from the leaf and hold it in a functional orientation (i.e. with the leaf-edge barbs facing away from the working end). In contrast, juveniles sometimes place the second cut/rip proximal to the first one. This results in the tool being held with the barbs facing towards the working end, which renders it non-functional. Furthermore, cut/rip actions may be of uneven depth and the tool cannot be removed from the leaf (Figures 3.3 and 3.4). At stage III juveniles reached adult-like technical skill in wide tool manufacture, carrying out the correct sequence of manufacture steps. Complete adult-like proficiency, however, was only reached at stage IV in the second year of life when juveniles’ speed of manufacture matched that of adults.

Successful tool use was also preceded by a period of ineffective probing that included failure to insert the tool into the hole or probing with a tool that was incorrectly inserted (Video 3.1). Even when probing with a correctly inserted and oriented tool juveniles mostly failed to extract meat during the first six months post-hatching. Juveniles' persistence at unsuccessful tool use might be an important factor in enabling animals to acquire complex behaviours. Kenward et al. (2006) found that their four hand-raised crows performed precursor actions and inserted objects into holes and crevices for several weeks before they managed to extract meat. They suggest that this behaviour might be the result of an inherited tendency to find certain actions rewarding even if they were not associated with food. Unrewarded persistence with tool use has also been observed in other animals. For example, neither chimpanzees nor capuchins appear to get reinforced other than by scrounging or tolerated theft before they crack their first nut after several years of interacting and practicing with the materials (Biro et al. 2006; de Resende et al. 2008). In contrast, young crows frequently get fed a large part of the meat that they had just watched a parent extract. The parental feeding might help explain why juveniles persist with unrewarded tool manufacture and use for many months until they begin extracting their own prey.

The extensive trial and error learning that I observed by the juvenile crows is also seen in the development of tool use in other species. Tebbich et al. (2001) suggested that woodpecker finches acquired tool use through a specific learning disposition that involves trial and error during a sensitive phase, without the need for social learning or reinforcement by obtaining food. Chimpanzees and capuchins also make a range of mistakes before successfully cracking their first nut (Inoue-Nakamura & Matsuzawa 1997; Hayashi et al. 2005; de Resende et al. 2008). According to action-perception theory (Lockman 2000), these mistakes are important to enable individuals to learn about the properties of objects and their causal relations. Young NC crows probably need to learn some kind of basic physical knowledge about pandanus tools and probe sites. Early uncoordinated ripping of Pandanus leaves might enable them to learn about their physical properties and that they have strong parallel fibers which facilitate the production of uniformly wide tools. By bending and folding pandanus tools into holes they experience that they are flat, flexible and only work when one end is inserted into the hole. Experimental work has shown that most adult NC crows do not pay attention to the presence and direction of barbs on wide pandanus tools (Holzhaider et al. 2008). Instead, they appear to obtain Stage III development above by associative learning about the correct sequence of manufacture actions required for successful food extraction.

An evolved disposition for certain action patterns (Kenward et al. 2005, 2006) combined with trial and error learning (Tebbich et al. 2001) appear to be sufficient to produce proficient stick tool use in NC crows and woodpecker finches. However, it is unlikely that such mechanisms alone can explain the complex tool skills seen in free-living crows. My results are consistent with the view that various forms of social learning play an important role in maintaining complex tool skills in NC crows (Hunt & Gray 2003, 2007). They show that juveniles have ample opportunity to learn socially via simple mechanisms such as local and stimulus enhancement. Juveniles visited tables together with one or both parents throughout their first year of life, but most commonly up to six months of age (Figure 3.1). While adult crows at tables generally manufactured their own pandanus tools to extract meat, juveniles up to six months of age predominantly used tools that were discarded or placed on the table after use by an adult (Figure 3.9). Many of these tools had been used by a parent immediately before the juvenile picked it up. This supports Kenward et al.’s (2006) finding that juveniles had a preference for objects that had been manipulated by a human demonstrator. I found no evidence of active teaching such as error correction by parent crows, but their tolerance to juveniles taking and using their tools is likely to have facilitated learning by the juveniles. Juvenile chimpanzees also frequently use tools that have been left by their mothers or other members of the community (Matsuzawa et al. 2001; Biro et al., 2006). Laboratory studies confirm that naïve subjects profit from using tools formerly used or manufactured by an experienced individual (Hirata & Morimura 2000; Hirata & Celli 2003). On Maré, pandanus tools are often left at the bases of pandanus leaves away from feeding tables where juvenile crows could easily find them.

Adult-made pandanus tools provide juveniles with opportunities to use suitable material for their early learning about tool use. Similarly, the presence of counterparts on leaves appear to facilitate juvenile tool manufacture by providing a starting point for the first rip. In this way juveniles would learn to start tool manufacture at a suitable place (typically one third to midway along the leaf edge in adult tool manufacture) rather than at the thin and damaged leaf tips. Leaves of Pandanus trees were often broken, or shortened by us if they impaired vision on the table. The high proportion of early juvenile tool manufacture starting at these damaged leaf edges (Figure 3.8) indicates that making the first cut into an intact leaf edge might be an important step in the development of tool manufacture. Counterparts could also guide juveniles about the ideal depth of a first cut into the pandanus leaf.

NC crow parents may also influence the emergence of juveniles' tool preferences via stimulus enhancement. Most adult crows have a strong, if not exclusive preference to manufacture and use either stick or pandanus tools (Hunt & Gray 2007). In the current study, all juveniles that developed a preference for pandanus tools had at least one parent with the same preference. Moreover, two juveniles of a pair in which both partners preferred to use stick tools also developed a preference for stick tools (Holzhaider et al. unpublished data). While basic stick tool use can develop without social learning and may be the ‘default’ tool use for NC crows (Kenward et al. 2005, 2006; Hunt & Gray 2007), my results are consistent with the idea that social input is necessary for the development of pandanus tool skills in the wild (Hunt & Gray 2003, 2007). Only one crow in this study, Abel, failed to develop a preference for pandanus tools, in spite of both his father and sibling preferring to make and use wide pandanus tools (Table 3.3). While Abel had shown signs of turning into a pandanus tool user up to six months of age, he then switched to predominantly using stick tools. Surprisingly, however, he manufactured two adult-like pandanus tools at around 12 months. The most likely explanation for this abrupt emergence of adult-like wide tool manufacture is that most of Abel’s learning took place away from the tables. From my earliest observations Abel’s sibling Cain was clearly the dominant bird, frequently attacking and chasing Abel off, and even taking tools from his bill and then discarding them. Abel may have avoided competition from Cain for access to pandanus tools at the feeding tables and relied on the more easily accessible stick tools away from the table.

Discarded tools and other artefactual material such as counterparts might not only enable juveniles to obtain early experience of tool use and manufacture, and influence their emerging preference of tool type, but also provide a way of transferring cultural information about specific tool designs. Juvenile crows might use tools and counterparts on pandanus leaves as templates for their own tool manufacture. In this way the wide, narrow and stepped tool designs could be faithfully transmitted between generations even in the absence of imitation. Template matching is a well-described process in songbirds. During a sensitive period young birds hear and memorise a tutor song. By practicing themselves they then gradually match their own song to the memorised template (Nottebohm 1984; Konishi 1985; Doupe & Konishi 1991). By this mechanism songbirds faithfully transmit local song dialect traditions (Mundinger 1980). A similar process of template matching might occur in the development of NC crow tool manufacture, with juveniles gradually adjusting the shape of their own tools to the designs manufactured by their parents.

A sensitive learning phase might also be involved in the acquisition of tool skills in NC crows. The fact that four out of five adult NC crows in the Nouméa zoo did not attempt to manufacture pandanus tools is consistent with this idea (Hunt et al. 2007). It seems likely that this period occurs within the first six months of a crow’s life when it spends the majority of its time with its parents and has direct access to parental tools and counterparts. A sensitive period during this time might also serve to imprint juveniles with the tool designs manufactured by their parents and reduce the possibility of horizontal transmission. Similar age effects have been shown in the acquisition of tool use and special feeding techniques in other birds and mammals. For example, woodpecker finches have been suggested to have a sensitive learning phase during which they acquire tool skills (Tebbich et al. 2001). Similarly, wild chimpanzees who did not begin to crack nuts by the end of a sensitive phase between the ages of three and five years of age never learned that skill later in life (Matsuzawa 1994; Biro et al. 2003).

The possibility of acquiring knowledge through niche construction and individual learning notwithstanding, many authors regard imitation as crucial for the faithful transmission of complex skills (Boyd & Richerson 1996; Tomasello 1999). Studies on nonhuman primates emphasise the importance of direct observation in the acquisition of tool use. Chimpanzees are frequently reported to ‘watch intently’ when, for example, their mother is engaged in nut cracking (Inoue-Nakamura & Matsuzawa 1997; Biro et al. 2006). Moreover, both chimpanzees (Hirata & Morimura 2000; Biro et al. 2003) and capuchins (Ottoni et al. 2005) prefer to observe animals that are more skilled than themselves, enhancing both their scrounging payoffs and social learning opportunities. In humans, watching and ‘paying attention’ is clearly crucial in order to faithfully learn from a demonstrator. I found that juvenile crows have ample opportunity to observe their parents’ tool skills. An important aspect in the master-apprenticeship theory of education (Matsuzawa et al. 2001) is the high tolerance shown to infants by their mothers and other members of the community. Similarly, crow parents are highly tolerant towards their own offspring, allowing them to observe their tool use close up and scrounge tools and even extracted meat. However, juveniles at feeding tables appeared to show limited interest in parental tool manufacture (Figure 3.2). The large peripheral field of vision of *Corvus* species makes it difficult to judge what they are actually observing (Emery & Clayton 2004a). Nevertheless, young NC crows rarely paid obvious attention to their parents’ pandanus tool manufacture or followed them into a tree where manufacture occurred. In contrast, they intently watched parents from close up when they were extracting meat from holes and, to a lesser extent, baited trees. However, my observations at feeding tables might have been biased because I separated the location of tool manufacture (the Pandanus tree) from the location of food extraction (the baited log). The juveniles usually just waited on the log where the food was for their parents to extract it. Moreover, feeding tables were probably highly salient as food sources so juveniles were more likely to stay on them even when food was also placed in the Pandanus tree later in the study. Away from feeding tables juveniles might watch tool manufacture more frequently by following parents into pandanus trees where both tool manufacture and use occur. Despite the juveniles’ apparent lack of attention, I found some evidence that they might have imitated certain parental motor patterns for tool manufacture. I identified three variants of wide pandanus tool manufacture used by adults (Video 3.3). While juveniles did not adopt their respective parents' preference, the distribution of the variants between the two families was very different (Figure 3.7). Variant A appeared to be the 'default' variant and was used by all crows to some degree. Variant B was strongly predominant in Pandora's family, while variant C was almost exclusively used by Adam and his offspring Cain. It is therefore possible that the juveniles learned about these variants by watching their parents and developed a preference for one of the variants they observed frequently. However, because of the small sample size I cannot exclude the possibility that this correspondence is due to chance. Further field research is needed to establish whether specific tool manufacture variants are faithfully transmitted within families.

In summary, the ontogeny of wide pandanus tool manufacture and use is a lengthy process similar to that of tool use in primates. The first three to six months in a young crow's life appear to be the most crucial period for the acquisition of tool skills. Juveniles spend most of this time with their parents, during which they often watch them using and manufacturing tools, get fed at a high rate, and commonly use discarded tools. From seven months onwards most juveniles have acquired the technical ability to produce wide pandanus tools of an adult-like shape, even if they still lack the speed of adults to manufacture tools and extract meat. Individual trial and error learning appears to play a major role in the development of pandanus tool manufacture, but juveniles also have ample opportunity to socially learn from their parents in a variety of ways. Parents scaffold the juveniles' environment early in their tool development by leading them to pandanus trees where they provide discarded tools and counterparts. This 'epistemic niche construction' (Laland et al. 2000; Odling-Smee et al. 2003; Sterelny 2006), might stimulate and facilitate early tool use and manufacture and enable the continuation of local design traditions.

Future research should concentrate on experimental work to investigate the possibility of template matching and the existence of a sensitive phase in the crows' ontogeny.

Supplemental Data: Videos 3.1-3.3. are available on the supplementary data CD included in this thesis and at http://media.brill.nl/behaviour/147/5-6/. For captions, see Appendix, p. 137.

4 Folk Physics – Do New Caledonian Crows attend to the Functional Properties of their Tools?[3]

Abstract

New Caledonian crows are the most proficient non-human tool manufacturers but the cognition behind their remarkable skills remains largely unknown. Here I investigate if they attend to the functional properties of the tools that they routinely use in the wild. Pandanus tools have natural barbs along one edge that enable them to function as hooking implements when the barbs face backwards from the working tip. In Experiment 1 I presented eight crows with either a non-functional ('upside-down') or a functional pandanus tool in a baited hole. Four of the crows never flipped the tools. The behaviour of the four flipping birds suggested that they had a strategy of flipping a tool when it was not working. Observations of two of the eight crows picking up pandanus tools at feeding tables in the wild supported the lack of attention to barb direction. In Experiment 2 I gave six of the eight crows a choice of either a barbed or a barbless pandanus tool. Five of the crows chose tools at random, which further supported the findings in Experiment 1 that the crows paid little or no attention to the barbs. In contrast, a third experiment found that seven out of eight crows flipped non-functional stick tools significantly more than functional ones. My findings indicate that the crows do not consistently attend to the presence or orientation of barbs on pandanus tools. Successful pandanus tool use in the wild seems to rely on behavioural strategies formed through associative learning, including procedural knowledge about the sequence of operations required to make a successful pandanus tool.

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[3] Based upon Holzhaider, J.C., Hunt, G.R., Campbell, V.M. & Gray, R.D. (2008). Do wild New Caledonian crows (*Corvus moneduloides*) attend to the functional properties of their tools? *Anim. Cogn. 11*, 243-254.

Introduction

Over the past decade there has been considerable controversy about the extent to which animals grasp the physical properties of their world ("folk physics" sensu Povinelli 2000). Explanations for how animals solve tool-related problems generally focus on either causal understanding (Limongelli et al. 1995) or associative learning (Visalberghi & Limongelli 1994; Povinelli 2000; Tebbich & Bshary 2004) (see Penn and Povinelli (2007) for a recent review). Chimpanzees' behaviour in the wild suggests that they might understand relevant functional properties of the tools they use. For example, in the Taï Forest, West Africa, they use sticks of different lengths to suit different tasks: short sticks to extract marrow from bones and longer ones to fish for termites or honey (Boesch & Boesch 1990). However, observations from wild behaviour alone are not sufficient to infer an understanding of how tools work. Experimental work with captive primates has shown that cotton-top tamarins (Hauser et al. 1999, 2002; Santos et al. 2003), vervet monkeys (Santos et al. 2006) and rhesus macaques (Santos et al. 2003) could all successfully choose between tools based on relevant and irrelevant features, with vervet monkeys showing similar abilities and limitations to those of chimpanzees (Santos et al. 2006).

The trap-tube experiment is a classic paradigm for exploring tool-related causal understanding. Two out of five chimpanzees were able to solve the problem by assessing the outcome of their action beforehand, which suggests some understanding of the relationship between an action and its outcome (Limongelli et al. 1995). In contrast, a series of experiments conducted by Povinelli and colleagues (2000) showed that chimpanzees lacked causal understanding for a range of tasks, including the trap-tube problem. They suggested that chimpanzees solved tasks by applying behavioural rules acquired through associative learning. Similarly, capuchin monkeys learned to solve the trap-tube problem by applying a distance-based behavioural rule to obtain the reward (Visalberghi & Limongelli 1994). However, more recent experiments with orangutans, chimpanzees, bonobos (*Pan paniscus*) and one gorilla (*Gorilla gorilla*) on a modified trap-tube showed that some individuals consistently avoided the trap only when it was functional (Mulcahy & Call 2006). This only occurred when they could rake the reward towards them rather than pushing it away as in the original experiment. Failure to solve tasks does not necessarily imply an inability to grasp the critical causal features (Silva et al. 2005), but compelling evidence of widespread causal understanding in primates is still lacking.

The pattern of primates solving problems via associative learning, rather than causal understanding, is mirrored in avian cognition. Woodpecker finches show flexible behaviour in using twigs and cactus spines as tools. For example, they modify tools according to their needs by breaking off side twigs which prevent insertion into holes (Eibl-Eibesfeldt 1961; Millikan & Bowman 1967). However, when confronted with cognitively more complex tasks like the trap-tube they, like primates, apply behavioural rules acquired through associative learning (Tebbich & Bshary 2004). Similarly, three out of seven non-tool-using rooks solved tasks with a modified trap-tube without an apparent understanding of relevant causal properties (Tebbich et al. 2007). Although one rook also solved several transfer tasks suggesting complex physical cognition, the possibility that it used learning strategies like rule abstraction could not be ruled out (Seed et al. 2006).

The most proficient non-human tool manufacturers are New Caledonian crows. These crows manufacture and use two different types of tools across their range: stick tools made from twigs and other similar material (Hunt 1996; Hunt & Gray 2002), and three different tool designs made from the barbed edges of pandanus leaves: wide, narrow and stepped (Hunt 1996). NC crows also craft hooked tools out of twigs in a process that can take well over one minute (Hunt 1996; Hunt & Gray 2004b). In laboratory tasks examining their tool-related cognition, NC crows chose tools of appropriate length (Chappell & Kacelnik 2002) and manufactured tools of appropriate diameter (Chappell & Kacelnik 2004). One individual, Betty, repeatedly bent novel material (straight wire) to extract a bucket containing food out of a vertical tube, thus apparently innovatively modifying tools in response to a specific need (Weir et al. 2002). She was subsequently presented with aluminium strips that required different techniques to turn them into functional tools. Instead of applying her previously learned wire-bending technique, Betty developed novel strategies to modify the strips into functional tools (Weir & Kacelnik 2006). Betty's modification skills suggested a grasp of folk physics exceeding that demonstrated by other non-human species. Wild NC crows routinely use pandanus tools as hooked implements. That is, when the birds use a pandanus tool the natural barbs along the edge of the tool are usually pointing away from the working tip. They are commonly observed using careful movements of the head that brush the barbs up against meat that was placed in holes (Hunt & Gray 2004a). Therefore, both circumstantial evidence from field observations and experimental evidence from captive birds suggest that NC crows may have considerable understanding of tool-related folk physics.

Most studies investigating the underlying cognitive mechanisms of animal tool use have been conducted in the laboratory using captive bred subjects or animals held captive for long periods of time (Visalberghi et al. 1995; Povinelli 2000; Chappell & Kacelnik 2002). However, the performance of such captive animals does not necessarily allow inferences to be made about the cognition underlying their behaviour in the wild (Emery & Clayton 2004a). In my experiments, I worked with crows that were either free-living or held captive for only short periods of time to assess their grasp of the folk physics involved in the tools they habitually manufacture and use in the wild.

NC crows' appropriate use of pandanus tools in the wild as hook tools suggests that they might understand the hooking affordance of barbs on these tools. I conducted two experiments on Maré Island with wide pandanus tools to assess if crows recognised that barbs are a crucial functional feature of these tools and if they attend to their directionality. Crows on Maré only make the wide pandanus tool design and it has recently been shown that individuals on the island generally specialise in using either stick tools or wide pandanus tools (Hunt & Gray 2003, 2007). In Experiment 1, I presented a crow with either an upside down (non-functional) pandanus tool in a baited vertical hole or a correctly orientated (functional) one. If birds recognised that barb direction was functionally relevant I expected them to rapidly flip the non-functional tool, but not the functional one. If they did this, the appropriate behaviour could have come from either a prior understanding of how barbs worked (strategy I), or a previously developed behavioural rule based on associating a functional tool with barbs facing away from the tool tip (strategy II). The design of Experiment 1 did not allow us to distinguish between these two strategies. Strategies I and II should be much more likely for crows that were pandanus tool specialists rather than stick tool specialists. Two other strategies based on a tool that does not work would be to either flip a tool if it is not successful at extracting the food (strategy III) or to replace it with a new one (strategy IV). I expected that strategies III and IV would produce similar latencies before flipping or discarding in barbs-up and barbs-down conditions. If crows developed either of strategies II-IV during the experiment rather than having acquired it previously, I would expect the latencies to decline noticeably over the course of the experiment. I also expected that crows which were stick tool specialists (i.e.

with limited or no experience of using pandanus tools) would be more likely to solve the task using strategy III or IV. The use of either of these strategies would be a strong indication that a crow did not recognize barbs were a crucial functional feature of pandanus tools.

In Experiment 2 crows had to choose between a pandanus tool with intact barbs and one with the barbs removed. This test investigated if crows associated barbs with a functional tool. If they did it would be consistent with the use of strategies I or II in Experiment 1. If they chose a tool randomly it would be consistent with the use of strategies III and IV. To assess how well the experimental findings fitted with pandanus tool use under more natural conditions, I also documented the behaviour of two free-living crows retrieving pandanus tools that had been dropped at tables. I investigated whether the crows had a preference to pick up and use tools in the correct orientation.

The main emphasis of my study was investigating NC crows' physical cognition associated with the use of pandanus tools. However, I also tested if NC crows could discriminate between a functional and a non-functional stick tool using the same methodology as in Experiment 1. I carried out this third experiment as a check on whether or not a crow's preference for a particular tool type might help explain its performance in Experiment 1. One end of the stick tool was straight (functional), but the other end had a short lateral-like extension which considerably restricted its movement in the hole (non-functional). The non-functional orientation of the stick tool in the hole should have been easier to detect mechanically, and also probably visually, than the non-functional orientation of a pandanus tool in Experiment 1. Therefore, I expected birds to flip an upside down stick tool more readily than an upside down pandanus tool.

Methods

Study Site and Subjects

The study site was situated in primary and secondary forest on the island of Maré, New Caledonia, about 5km inland from Wabao village. Subjects were nine wild New Caledonian crows: eight males (Epi, Abraxas, Pierrot, Sylvester, Brando, Bender, Max and Arnie) and one female (Pandora). Brando was two years old at the time of testing and Pierrot was a subadult around 1.5 years old. Both Brando and Pierrot were nutritionally independent. The other seven birds were adults. All crows except Pandora were marked with coloured leg bands for individual recognition. Six of the nine crows were tested individually in outdoor aviaries with no visual access to other crows. The aviaries were roughly 2m x 4m and 3m high. Crows were fed an ad libitum diet of cooked rice, moistened dog biscuits, fresh meat and papaya (*Carica papaya*). Food was removed at least 1 hr before experimental trials began. Crows' change of body weight during captivity was less than 5 % of their weight at capture. The six captive crows were caged from 29-49 days before being released. All birds were observed frequently after their release and showed no obvious deleterious effects of being held in captivity.

Three of the nine crows (Pandora, Epi and Bender) were tested at feeding tables set up in the forest. Pandora was unbanded, but she usually visited a table together with her banded partner Epi. All nine crows had probably visited feeding tables before they were tested here between October 2003 and December 2005. Epi only participated in Experiment 3 and Bender only participated in experiments 1 and 2. Most of the trials were recorded on video for later analyses, but some for Bender, Pandora, Arnie and Sylvester could not be filmed because of camera failure.

Experimental Setup and Procedure in the Aviary

A dead log with vertical holes drilled in it was placed on a feeding table around 1m high. The holes were 6-7cm deep and 2.5cm in diameter. A piece of meat was placed at the bottom of one hole. The depth of the hole meant that the birds could only extract the meat with a tool. Testing took place in morning and afternoon sessions. A crow was usually given experiments 1-3 sequentially (see below), but for Abraxas, Pierrot and Pandora the order was 1, 3 and 2. All experimental tools were made by us and their shape and size was consistent with that of tools crows made at the site (Hunt & Gray 2003).

Crows at the Maré study site have a strong, or even exclusive, preference to use either stick tools or pandanus tools (Hunt & Gray 2007). As these preferences might explain behavioural variation between individuals in these experiments I first established which tool type, if any, a crow preferred to use. To do this, I stood a stick tool and a pandanus tool upright and adjacent to the baited hole. Each crow was given 24 trials in four blocks of six trials. For each trial I recorded which of the two tools was first inserted into the baited hole. Trials lasted 10 minutes. If a crow extracted the meat in less time, I only started the next trial after a full 10min had elapsed.

Experiment 1: Pandanus Tool flipping

A barbed pandanus tool ca. 12cm long and 0.5cm wide was placed in the baited hole. My objective was to test each crow in six blocks of five trials. In each trial, a crow was required to use the provided tool to extract the meat. A very small piece of meat was placed next to the baited hole immediately prior to each trial to attract a bird’s attention. A trial began as soon as the crow touched the tool with its bill. In trials 1-10 and 21-30, the tool was turned upside down (barbs-down condition) so the natural barbs along the edge of the tool were pointing towards the working tip. This usually made the tool non-functional for meat extraction unless it was “flipped” around. A flip was defined as a deliberate and quick turning around of the tool. This could be achieved by putting the tool down and picking it up again by the other end, or by turning it around while holding it in the bill (Video 4.1). In some trials a crow dropped a tool and then picked it up at the end that it could most conveniently reach. If the tool orientation was now reversed, the action was recorded as a non-intentional flip. On very hot days a crow sometimes extracted meat with the non-functional tool because it stuck to the end of the tool. I counted these trials as “false trials” and compensated for them with additional trials to ensure that all birds received a similar number of trials with non-functional tools. In control trials 11-20 the tool was placed in the hole with the barbs pointing upwards (barbs-up condition).

A pandanus tree was placed next to the feeding table to allow crows to manufacture their own tools if they did not succeed with the one provided. The aviary had a natural floor and although I carefully attempted to remove all potential tools from the ground crows sometimes found sticks and roots there to use as tools. The number of trials varied because of lack of motivation (Abraxas, Pierrot, 1 trial each) or an additional trial added after block 6 to compensate for a false trial in block 2 (Arnie).

From video footage I recorded the length of time that each crow probed with a tool before it flipped it, discarded it, extracted meat with it or gave up. Probing time began when a crow inserted the tool in the hole.

Experiment 2: Pandanus Tool Selection

Crows were given the choice of two pandanus tools: one that was barbed (functional) and one that had the barbs removed (non-functional) (Figure 4.1a). Both tools were presented upright and equidistant from the baited hole, with the flat side of each tool facing the log. The positions of the barbed and the barbless tools were semi-randomised to ensure that each tool was presented equally often in both positions, and no more than two consecutive trials in the same position. The distance from the tools to the log was 20 cm. Each crow received 24 trials in four blocks of six trials. The first tool that a crow inserted into the baited hole was recorded as its preferred one.

Experiment 3: Stick Tool Flipping

The methodology in this experiment was the same as in Experiment 1. However, instead of a pandanus tool I presented a stick tool. Crows on Maré commonly make stick tools from *Olea paniculata* trees (see examples of these tools in Hunt 1996; Hunt & Gray 2002). One end often has a lateral-like extension that was part of the adjoining twig (wide end). In the wild, crows generally use the narrow ends of these tools as the working end. I made *Olea paniculata* stick tools for this experiment similar to the shapes of the different-ended tools that crows made at the site (Figure 4.1b). The end with the lateral-like extension (non-functional) could be inserted into the hole but it did not allow free movement and severely restricted the tool’s effectiveness. The hole was sufficiently wide to allow a crow to look into it and potentially assess the operation of the tool. As in Experiment 1, when a crow extracted meat with the non-functional end I recorded a “false trial”. Pierrot only received 19 trials in the extension-down condition because of lack of motivation.

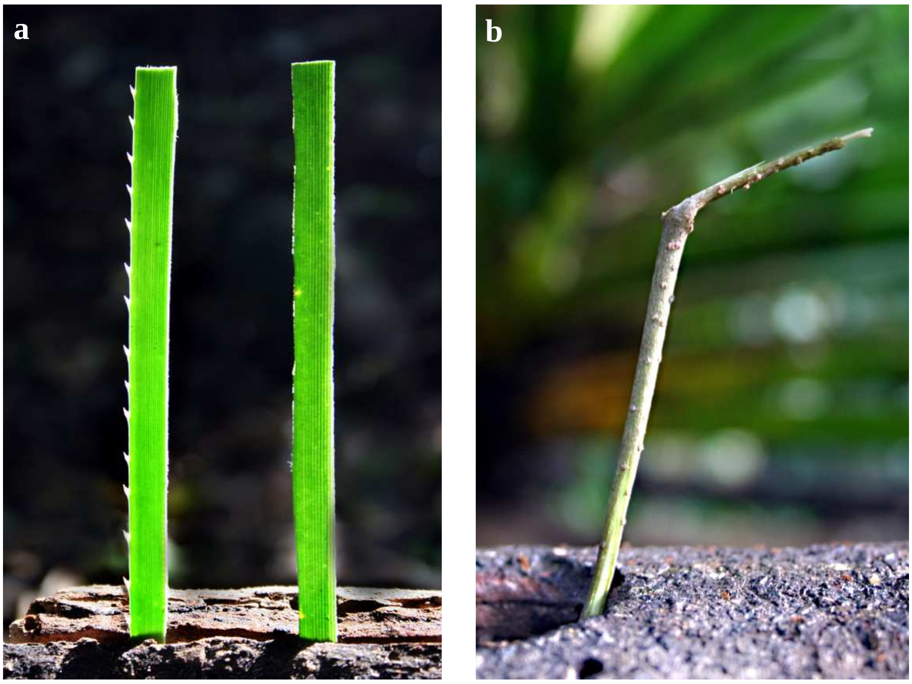


Figure 4.1. Experimental tools. a) Example of a barbed (left) and a barbless (right) wide pandanus tool. The barbed tool is presented in the barbs-up, functional condition. b) Stick tool with lateral-like extension presented in the extension-up, functional condition.

Experimental Procedure at Forest Sites

The methodology used with the three free-living crows varied slightly to that used in the aviary. Given that more than one crow could visit a feeding table at the same time, in experiments 1 and 3 I baited up to eight holes to ensure that the experimental crow had meat to extract. At the table where Pandora and Epi fed, I provided both stick tools and pandanus tools (2 of each type). This was because Epi usually arrived at the table before Pandora. He would then discard the pandanus tool and get the meat with a stick before Pandora could be tested. Experiment 1 for Pandora and Experiment 3 for Epi were therefore conducted simultaneously. Tool-type preference for Pandora, Epi and Bender was established during the course of the experiments. After Pandora had completed Experiment 1 I stopped providing pandanus tools to encourage her to use stick tools for

Experiment 3. In Experiment 2 I also baited several holes, but provided only the two pandanus tools (barbed and barbless) as for the methodology in the aviary. I aimed to give the three crows the same number and organisation of trials as in the aviary, but this was not always possible because testing depended on when they visited the tables. Bender received only 19 barbs-down trials in Experiment 1 and Pandora received only 18 extension-down trials in Experiment 3. They completed nine and seven trials, respectively, in Experiment 2. For Bender, two trials from Experiment 1 were excluded from the analyses because of unclear footage.

Observations of Free-Living Crows at Feeding Tables

Crows on feeding tables often pick up and use pandanus tools that have been dropped by either themselves or other birds. I used video footage of Bender and Pandora to assess if they picked up tools in the correct orientation. I recorded the orientation of all tools that they picked up (i.e. barbs-up or barbs-down). If they had put the tool down just prior to picking it up (e.g. to eat meat), I also recorded the tool’s orientation just before it was put down.

Data Analysis

I used 2 x 2 contingency tables to analyse tool flipping in Experiments 1 and 3. I tested separately each crow that flipped tools, placing its data in a row (barbs-up versus barbs-down) by column (flip versus no-flip) configuration. As cell sizes were often small (<5), I carried out the tests for independence with Fisher’s exact probability test. To compare latencies to flipping between the barbs-up and the barbs-down conditions and between probing times of crows with different behaviour in Experiment 1, I used Mann-Whitney U-Tests. For the latter, I adjusted the probability level to 0.016 with a Bonferroni correction to account for multiple pair-wise tests. Although the Bonferroni correction is conservative, it is suitable for sample sizes less than five (Bender and Lange 2001). I used Spearman's rho correlation to look for an association between probing time in the barbs-down condition and trial number. I used a binomial test to determine whether a crow had a preference when choosing between tool types, if it had a side bias and if it preferred to pick up tools in the barbs-up orientation. Tests for tool preference (stick tool versus pandanus tool), side biases and differences between probing times were two-tailed. All other tests were one-tailed.

Results

Four of the six aviary crows had a significant preference for using either stick tools or pandanus tools (binomial tests, two-tailed, $p = 0.001$ for Max, $p < 0.001$ for Abraxas, Sylvester and Brando. Sample sizes in Figure 4.2). Epi, Pandora and Bender were not given the tool selection test. However, Pandora and Bender always used pandanus tools at the feeding tables, and Epi always used stick tools. Pierrot and Arnie did not have a significant preference for either type of tool. Nevertheless, I recorded Arnie as a pandanus tool user because whenever he failed to extract meat with a provided tool in the experiments he replaced it with a self-made pandanus tool. No crow that was tested in the aviary had a significant side bias when choosing between stick and pandanus tools.

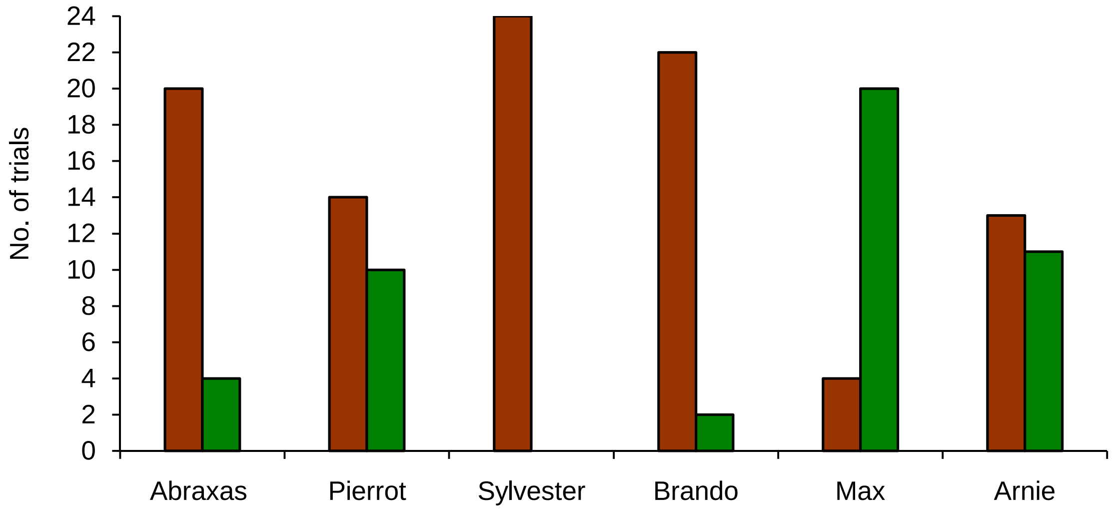


Figure 4.2. Crows' choice of either a stick tool (black bars) or a pandanus tool (white bar) when tested in the aviary. All birds except Pierrot and Arnie had a significant preference for one type of tool.

Experiment 1: Pandanus Tool Flipping

Four out of eight crows flipped the pandanus tool (Table 4.1). Of these four birds (Sylvester, Brando, Bender and Max), only Bender and Max flipped the tool significantly more often in the barbs-down condition (non-functional) than in the barbs-up condition (functional) (tests of independence in Table 4.1). Sylvester flipped the least of the four crows, doing so three times in both the barbs-down and the barbs-up conditions. Flipping in the barbs-up condition occurred more often in block 3 (12 out of 20 trials) than in block 4 (4 out of 20).

Table 4.1. The frequency of flips in Experiment 1

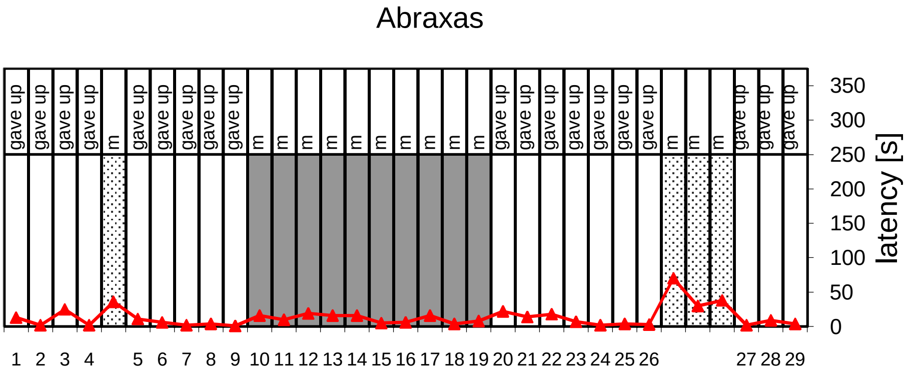
Crow	Barbs-down		Barbs-up		Barbs-down		Fisher exact probability test
	Block 1	Block 2	Block 3	Block 4	Block 5	Block 6	
Abraxas	0/4	0/5	0/5	0/5	0/5	0/5	no flips
Pierrot	0/5	0/5	0/5	0/5	0/5	0/4	no flips
Sylvester	2/5	1/5	2/5	1/5	0/5	0/5	$N = 30, p > 0.05$
Brando	0/5	5/5	3/5	2/5	5/5	5/5	$N = 30, p > 0.05$
Bender	5/5	4/4	4/5	1/5	4/4	5/5	$N = 28, p < 0.05$
Max	4/5	5/5	4/5	0/5	5/5	5/5	$N = 30, p < 0.05$
Arnie	0/5	0/4	0/5	0/5	0/5	0/6	no flips
Pandora	0/5	0/4	0/5	0/5	0/5	0/6	no flips

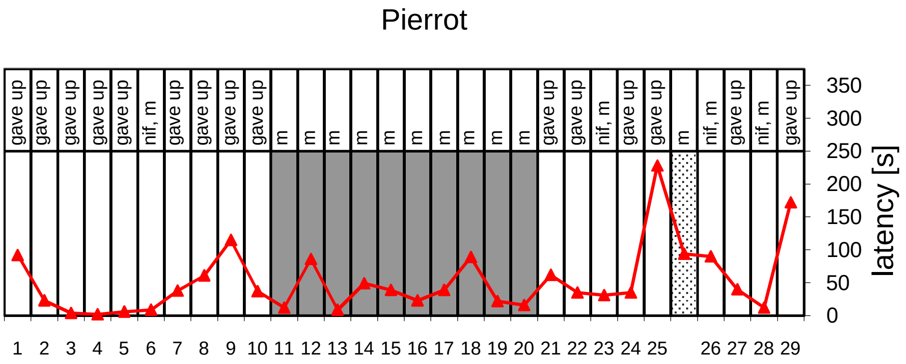
The frequencies are shown for each block within each condition. For example, 2/5 indicates that the crow flipped the tool in two out of five trials. I used the Fisher exact probability test to compare flipping frequency between the barbs-up and the barbs-down (blocks 1, 2, 5 and 6 combined) conditions. Trials were excluded if a crow extracted meat without flipping in the barbs-down condition ($N = 20$ trials)

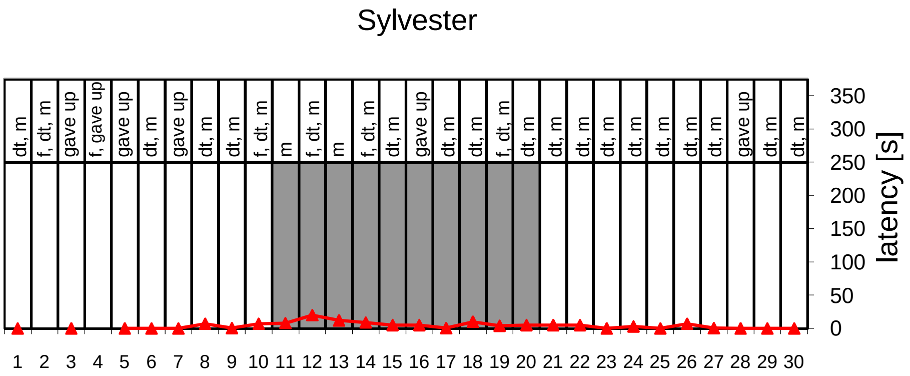
A detailed look at the behaviour of individual crows provided an insight into the cognitive strategies behind the tool flipping. Bender, Max and Brando regularly flipped the barbs-down tool (18, 19 and 15 times, respectively) then generally retrieved the meat. Only Max showed a significant correlation between latency to flip and trial number. His probing time until flipping decreased with trial number ($r_s = 0.85$, $N = 20$, $p < 0.001$), indicating that he might have acquired the ability to flip pandanus tools in the course of the experiment. Brando did not flip the barbs-down tool in trials 1-5, but always flipped it from trial 6. However, Bender, Max and Brando also flipped up to five tools in the barbs-up condition, indicating that the direction of the barbs alone did not determine their decision to flip a tool. If the crows attended to the direction of the barbs, flips in the barbs-down condition should occur quickly. Flips in the barbs-up condition should only occur, if at all, after prolonged and unsuccessful probing. However, there was no significant difference in the latencies to flips between the barbs-down and the barbs-up condition (Mann-Whitney U-test; Bender: $U = 10$, $N_1 = 12$, $N_2 = 4$, $p = 0.09$; Max: $U = 38$, $N_1 = 19$, $N_2 = 4$, $p = 0.97$; Brando: $U = 23$, $N_1 = 15$, $N_2 = 4$, $p = 0.44$). Whenever the birds flipped a barbs-up tool and failed to get meat with it, they flipped it back again so it was functional. In trials 11 and 12, Max flipped the tool six and four times, respectively, until he extracted meat.

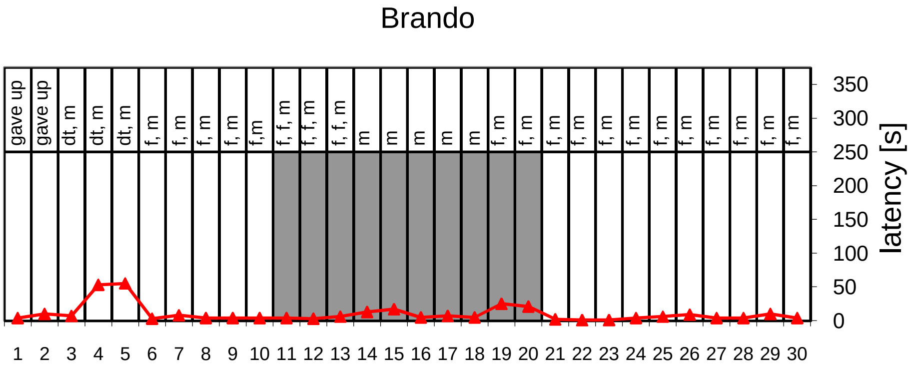
Four birds (Abraxas, Pierrot, Arnie and Pandora) never flipped the pandanus tool in either condition. The behaviour of these crows in the barbs-down trials varied considerably. In 10 out of 20 trials Pandora abandoned attempts to extract the meat after unsuccessfully trying with the provided tool. She made a replacement pandanus tool in nine trials and extracted meat with seven of these tools. In 19 trials after initially trying to get the meat with the barbs-down tool Arnie extracted it with a replacement pandanus tool that he had made. Both Pandora and Arnie only made replacement tools in the barbs-down condition. Abraxas ($N = 19$) and Pierrot ($N = 15$) often discarded the tools without getting any replacement. However, in four trials Pierrot picked the discarded tool up from the ground and extracted meat with it. The four non-flipping crows extracted meat with the barbs-down tool up to five times between valid trials by vigorous probing until the meat stuck to the non-functional end.

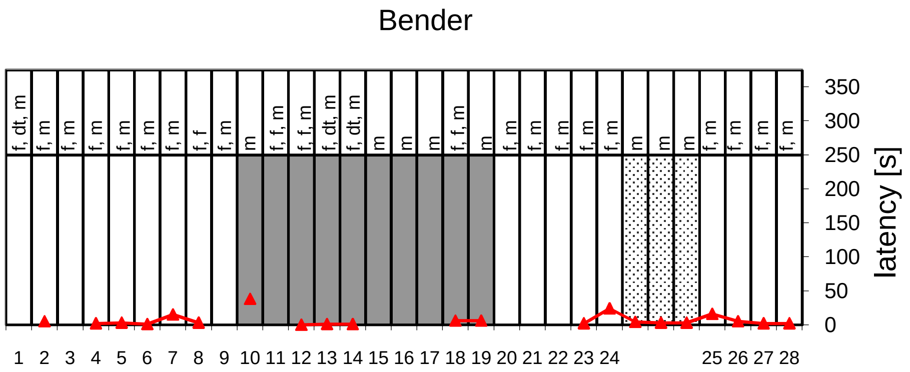
Figure 4.3 (following page): Trial by trial description of behaviour in Experiment 1 in the barbs-down (white bars) and barbs-up (grey bars) conditions. Stippled bars indicate trials in which crows extracted meat with the barbs-down tool (false trials). Latency gives the time a bird spent probing the hole with the tool until the first action. Depending on the trial, the first action is either meat extraction, flipping, or discarding the tool. For Pandora, Bender and Sylvester, latency data are missing in some trials. In all trials, crows probed the hole with the experimental tool. The text above the bars describes the sequence of behaviour in the trial. For example, the sequence “f, dt, m” indicates that the crow probed for the time indicated by latency before flipping the tool (f), then used a different tool (dt) to extract meat (m). A non-intentional flip (‘nif’) occurred when a crow dropped the tool and picked it up immediately in the opposite orientation. When choosing a different tool, Sylvester and Brando always chose a stick and Bender, Arnie and Pandora always chose a pandanus tool.

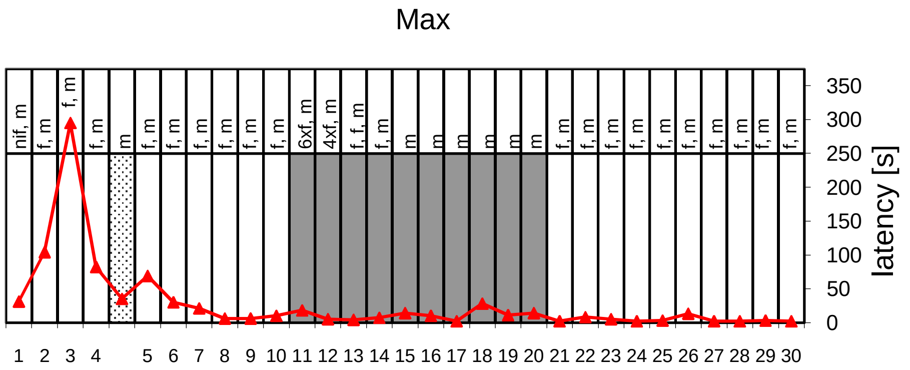

Abraxas

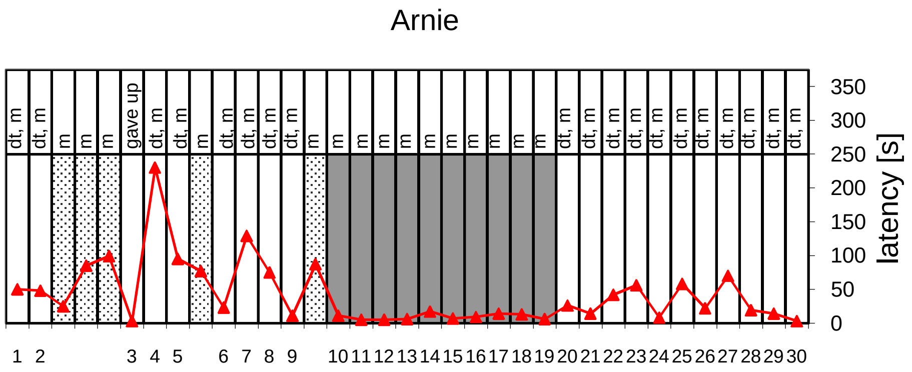

Pierrot

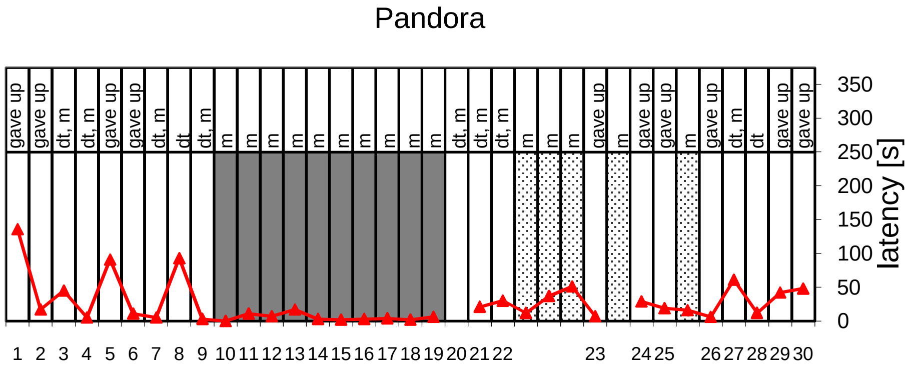

Sylvester


Brando


Bender


Max


Arnie


Pandora

A crow's tool preference (Figure 4.2) was not closely associated with its ability to flip a non-functional pandanus tool. For example, Brando preferred stick tools and flipped pandanus tools, whereas Pandora and Arnie preferred pandanus tools but never flipped them. However, there were interesting associations between probing times of birds and different flipping behaviour. I identified three behavioural groups: those with a preference for stick tools that never or rarely flipped (Abraxas and Sylvester), those with a preference for pandanus tools that never flipped (Pandora and Arnie), and those that regularly flipped (Bender, Max and Brando) (Figure 4.4).

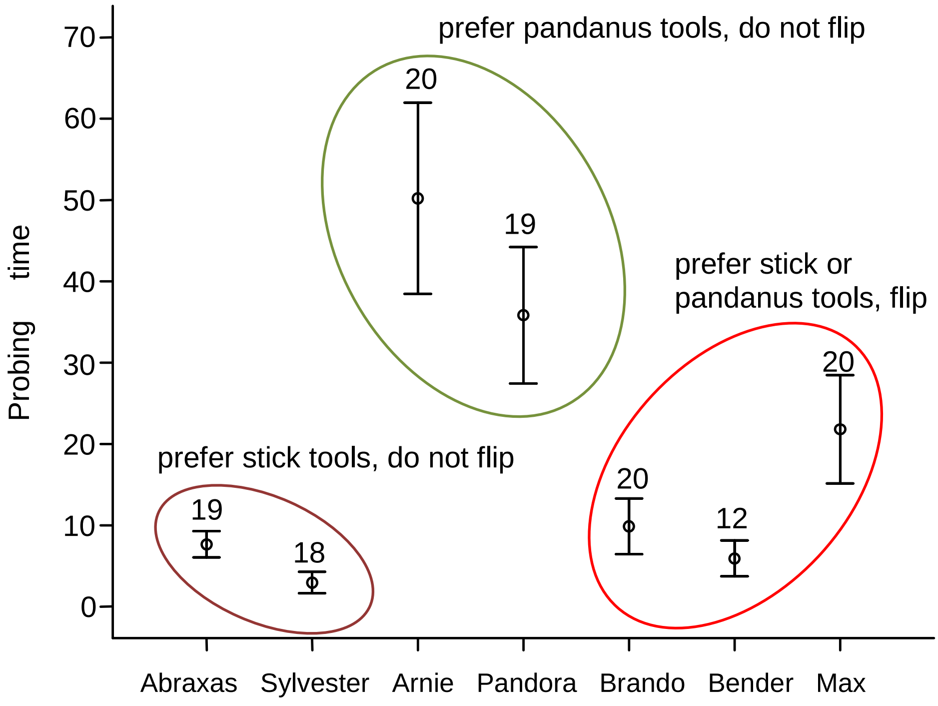


Figure 4.4. Mean latencies (± 1 standard error) until flipping or abandoning a barbs-down pandanus tool. Sample sizes are above the error bars.

Pierrot did not fit into any of these groups because he did not flip and had no preference for a particular tool type. All three pair wise-tests of probing times between the groups were significant. Non-flipping crows Pandora and Arnie (*Mdn* = 26) probed longer than the flipping group (Bender, Brando and Max, *Mdn* = 4) (Mann-Whitney, $U = 370$, $N_1 = 39$, $N_2 = 51$, $z = -5.09$, $p < 0.001$, $r = -0.54$). Abraxas and Sylvester (*Mdn* = 2.5) spent less time probing than both the flipping group ($U = 661$, $N_1 = 38$, $N_2 = 51$, $z = -2.57$, $p = 0.01$, $r = -0.27$) and the non-flipping group that preferred pandanus tools ($U = 137$, $N_1 = 38$, $N_2 = 39$, $z = -6.17$, $p < 0.001$, $r = -0.7$).

Experiment 2: Pandanus Tool Selection

Crows overall chose the barbed tool significantly more than the barbless tool, doing so in 65% of all trials (binomial test, one-tailed, N = 112, p = 0.002) (Figure 4.5). However, only Sylvester had a significant individual preference for the barbed tool (binomial test, one-tailed, N = 24, p = 0.01). Abraxas and Arnie had a significant side bias and were excluded from the above analyses (binomial test, two-tailed, N = 24, p < 0.001 for both birds). When choosing the barbless tool, Abraxas, Pierrot, Sylvester and Arnie usually discarded it after trying to get meat. They then either used the barbed tool or extracted meat with another tool that they found in the aviary. Bender, Max and Brando flipped the barbless tool in some trials before discarding it (3, 3 and 7 times, respectively). In contrast to Pandora's lack of pandanus tool flipping in Experiment 1, she flipped one barbless tool three times when trying to extract meat with it.

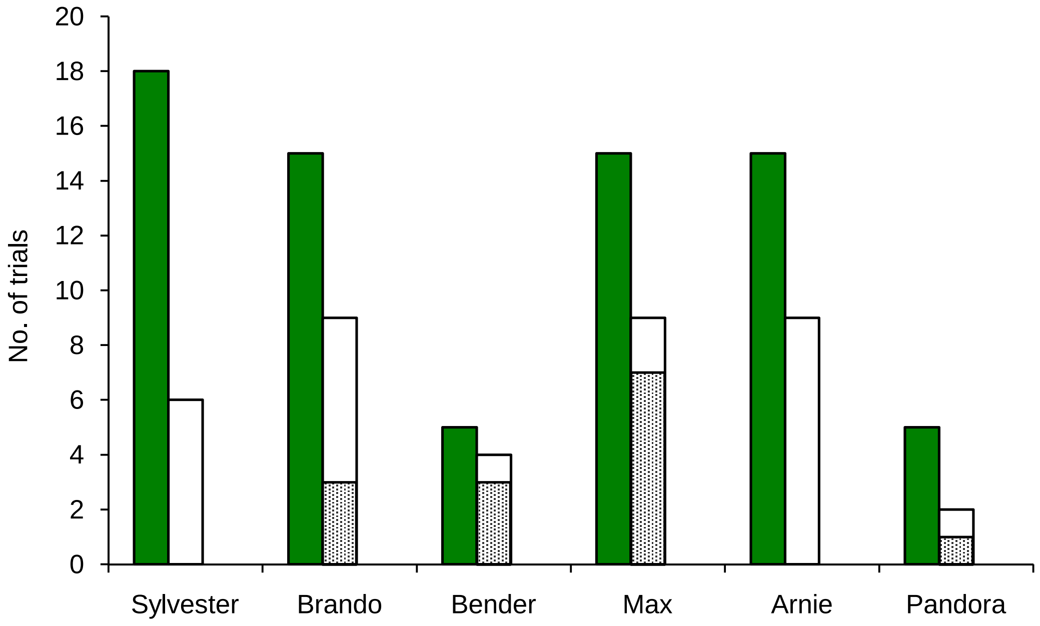


Figure 4.5. Crows' choice of either a barbed (green bars) or barbless pandanus tool (white bars). Only Sylvester had a significant preference for a particular tool. The grey region indicates the number of trials in which the birds flipped the barbless tool.

Experiment 3: Stick Tool Flipping

Crows flipped the non-functional stick tool much more than the non-functional pandanus tool. All eight birds flipped the stick tool at least once in the extension-down (non-functional) condition (Table 4.2). Seven of these crows flipped the tool significantly more often in the extension-down condition (non-functional) than in the extension-up condition (tests of independence are in Table 4.2). Only Sylvester flipped the tool in the extension-up (functional) condition; this occurred twice in block 3 (Table 4.2).

Table 4.2. The frequency of flips in Experiment 3

Crow	Extension-down		Extension-up		Extension-down		Fisher exact probability test
	Block 1	Block 2	Block 3	Block 4	Block 5	Block 6	
Epi	6/6	6/6	0/5	0/5	3/3	4/5	$N = 30, p < 0.01$
Abraxas	5/5	5/5	0/5	0/5	2/5	4/5	$N = 30, p < 0.01$
Pierrot	0/4	0/5	0/5	0/5	1/5	0/5	$N = 29, p = 0.65$
Sylvester	5/5	5/5	2/5	0/5	5/5	5/5	$N = 30, p < 0.01$
Brando	5/5	5/5	0/5	0/5	5/5	5/5	$N = 30, p < 0.01$
Max	5/5	5/5	0/5	0/5	5/5	5/5	$N = 30, p < 0.01$
Arnie	0/5	3/5	0/5	0/5	1/5	3/5	$N = 30, p = 0.04$
Pandora	0/4	0/4	0/5	0/5	4/5	5/5	$N = 28, p = 0.01$

The frequencies are shown for each block within each condition. For example, 6/6 indicates that the crow flipped the tool in six out of six trials. I used the Fisher exact probability test to compare flipping frequency between the barbs-up and the barbs-down (blocks 1, 2, 5 and 6 combined) conditions. Trials were excluded if a crow extracted meat without flipping in the extension-down condition ($N = 4$ trials).

Abraxas, Epi, Sylvester, Brando and Max sometimes flipped the extension-down tool without any attempt to extract the meat first (in 7, 5, 3, 2 and 2 trials, respectively). That is, they pulled the tool out of the hole without any obvious probing movements and in less than 1s. Sylvester and Max did this on the first trial of the experiment, but repeated the behaviour only in later trials. Pandora was the only crow that changed strategies over the course of the experiment. She did not flip the extension-down tool in the first ten trials, but did so nine times in trials 21-30. Four birds sometimes used an interesting alternative strategy to retrieve the meat: rather than flipping, they modified the non-functional end with their bill by removing or reducing the lateral-like extension (Figure 4.6). Pierrot used this strategy in 16 out of 19 extension-down trials. In two trials he worked on both ends and broke the tool into several pieces, none of which was suitable to extract meat. He flipped the tool only once (trial 24). Abraxas flipped the tool at the hole in trials 1-10 and 21-22 of the extension-down condition. In trials 23-28, he took the tool to a perch to either flip it (two trials) or modify it (four trials) before flying back to the hole and extracting the meat. Arnie attempted to modify the tool in 10 trials and succeeded in taking off the extension in five trials. After tool modification, both Arnie and Abraxas surprisingly used the non-extension end to extract the meat. Pierrot, though, usually used the modified end to extract meat.

In the extension-up condition, the birds mostly extracted the meat without flipping or modifying the tool. Sylvester flipped the tool in two trials after spending some time trying to extract meat. In one of the two trials, he retrieved the meat with the extension-down tool. In the other trial, he flipped the tool a second time and extracted the meat. Pierrot removed the extension twice before using the tool to extract the meat.

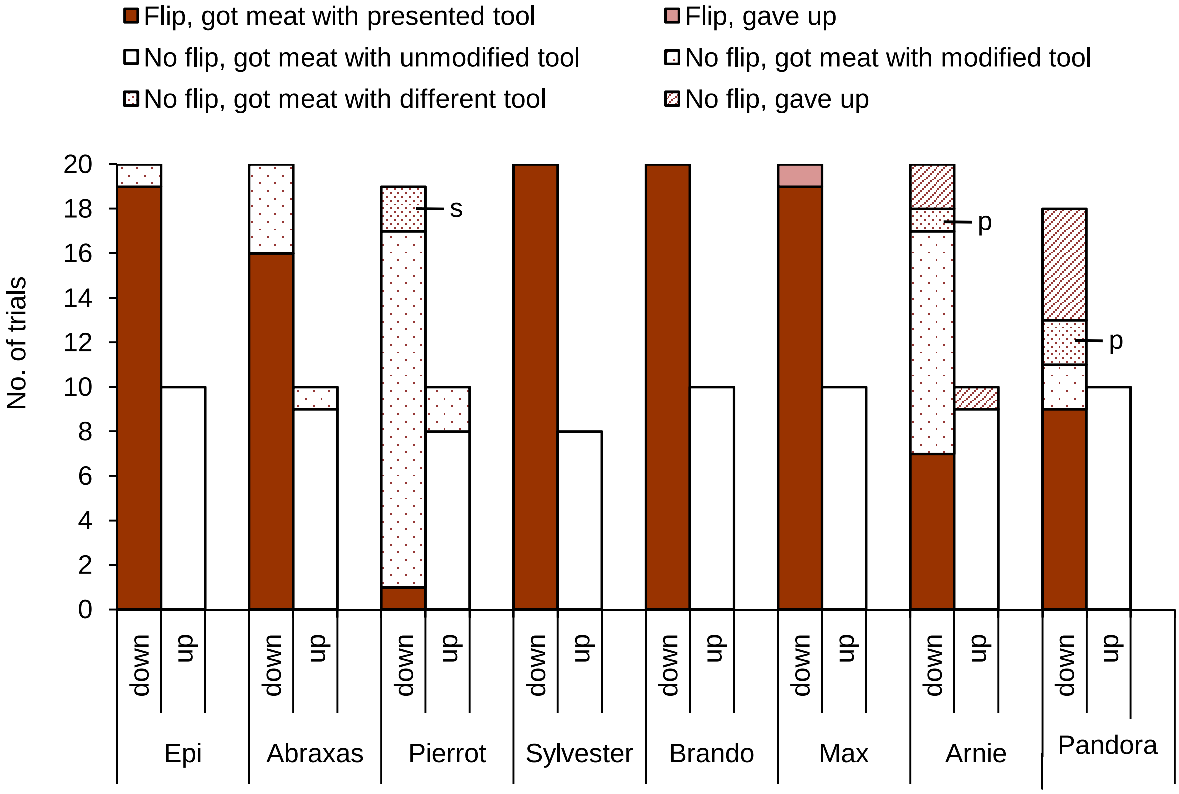


Figure 4.6. Detailed summary of the stick tool flipping trials in the extension down and up conditions for each crow. (s) and (p) indicate whether the crow used a stick tool or pandanus tool as a replacement tool. Trials in which a crow extracted meat with an extension-down tool (Epi, Pierrot: 1; Pandora, Sylvester: 2) were regarded as “false trials” and excluded from the figure.

Observations of Picking up Tools at Feeding Tables in the Wild

I documented 587 occasions in which Pandora and Bender picked up a pandanus tool from a table or underneath it. In 502 of these cases they had previously used the tool with the barbs facing upwards to get meat from a vertical hole, put the tool down beside themselves to eat the meat, then picked up the tool to probe again. In the large majority of these cases (96%), the two crows picked the tool up in the same orientation that they had used it just before putting it down (i.e. functionally). However, when they picked tools up that they had not recently used, only Bender had a significant preference to pick up the tool in a functional orientation (binomial test, one-tailed; Bender: $N_{barbs\text{-}up} = 16$, $N_{\text{barbs-dow}} =$ 7, $p = 0.047$; Pandora: $N_{barbs\text{-}up} = 36$, $N_{barbs\text{-}down} = 26$, $p = 0.12$).

Discussion

Observations in the wild suggest that New Caledonian crows make and use pandanus tools because of their hooking affordances (Hunt 1996; Hunt & Gray 2002, 2004b). Somewhat surprisingly, I found that individual crows do not consistently attend to the barbs that are a crucial functional feature of pandanus tools.

I identified four possible behavioural strategies that a crow could use to solve the tool problem in Experiment 1: causal understanding about how barbs worked (strategy I), associating barb direction with functionality (strategy II), flipping the tool if it did not work (strategy III), and replacing the tool (strategy IV). In Experiment 1, four out of eight crows flipped the tool when it was presented in the non-functional condition. However, their behaviour, particularly their tendency to flip the tool even in the functional condition, did not support an appreciation of the relevance of barbs (strategies I and II). The four non-flipping birds either lost interest or replaced the non-functional tool with one that they made from the pandanus tree that I provided. The inference that the crows lacked an understanding of the functional relevance of the barbs was supported by the results of Experiment 2, where only one individual chose the barbed tool significantly more than the barbless one. The observations of Pandora and Bender picking up tools at tables in the forest outside the experimental setup provided further support for this inference. Although Bender picked up tools that he had not recently used more often in a functional orientation, Pandora did not.

Jungle crows (*Corvus macrorhynchos*) are reported to have a near-field visual acuity of 8.4 cycles/degree in a distance of 23cm (Yamamoto et al. 2001). Given that this is the equivalent of an ability to distinguish between features at least 0.5mm apart, detecting barbs on pandanus tools and the direction that they face should be well within crows' visual capabilities.

The behaviour of the crows in Experiment 1 gave an insight into the strategies crows deploy to successfully use pandanus tools as hooking implements. Of the four crows that flipped pandanus tools, only three (Bender, Max and Brando) repeatedly did so in any successful way; two of them flipped the barbs-down tools significantly more often than the barbs-up tools. The flipping seemed to be based on the strategy of flipping a tool if it does not work (strategy III), rather than an understanding of the hooking affordance of the tools (strategy I) or an association between barb direction and functionality (strategy II). There are three reasons for this. First, the use of strategies I or II is unlikely because all three crows flipped tools even when they were presented in the functional condition. Second, the latencies to flip functional tools were no different from the latencies to flip non-functional tools. Third, five out of six individuals chose tools at random in Experiment 2, and four of these five crows also flipped barbless tools.

In contrast to the birds that had a strategy of flipping pandanus tools, Pandora and Arnie used a strategy of tool replacement. The sequence of actions used by experienced crows to manufacture a tool usually means that it is held in the correct orientation when first removed from the leaf (Hunt & Gray 2004a). This occurs because crows usually make the first rip towards the leaf tip, then they remove the tool by a rip towards the leaf base. As barbs face towards the tip of the leaf the tool is initially held in a functional orientation. This was the case whenever Pandora and Arnie made a replacement tool. The initial association between correct tool orientation and appropriate manufacture procedure is generally maintained even when a crow briefly puts down a pandanus tool. The use of the appropriate manufacture and handling procedures by experienced crows is probably why I have rarely observed crows flipping self-made pandanus tools at feeding tables in the wild. Inexperienced juveniles on Maré, though, frequently manufacture pandanus tools with the barbs initially facing towards the working tip. Crows may develop a consistently correct manufacture procedure from a learned association between the procedure and a tool that works (i.e. correctly orientated). Work with hand raised NC crows (Kenward et al. 2005, 2006) showed that although they may have inherited predispositions for basic tool use, they require extensive practise before reaching adult proficiency. It seems likely, therefore, that proficiency in pandanus tool use depends heavily on learning procedural knowledge about the appropriate manufacturing sequence.

Seven of the nine experimental crows had a clear preference for using either stick tools or pandanus tools. Their preferences were not closely related to their performance in Experiments 1 or 2. However, there was an interesting association between tool preference and probing times for birds that never, or rarely, flipped pandanus tools. The two crows that preferred pandanus tools (Pandora and Arnie) probed significantly longer until discarding the tool than the two that preferred stick tools (Abraxas and Sylvester). The lack of any successful flipping by the latter two birds might have come from poor motivation because they flipped stick tools. Previous experience in the wild that pandanus tools usually work might explain why Pandora and Arnie did not flip tools.

Crows’ preferences for using either stick or pandanus tools were also not closely related to their performance in Experiment 3 with stick tools. The performance of the crows in Experiment 3 suggested that the task was strikingly different to the task in

Experiment 1 with pandanus tools. All but one crow flipped the stick tool significantly more often in the non-functional condition. Five crows also sometimes flipped tools before any obvious attempt to use them, therefore they may have assessed the utility of the tool before using it. Two reasons may explain crows' greater success in Experiment 3 than in Experiment 1. First, it was probably easier to recognise that the extension on the working end made the tool non-functional, either by visual and/or mechanical means. Second, both ends of a straight stick can potentially function as a narrow probe, which may encourage flipping and the use of both ends to extract prey. Free-living crows are often observed to flip their own stick tools if they encounter problems extracting prey. Experiment 3 showed that modification is also a strategy that crows can use to make a stick tool functional. Four birds attempted to remove or reduce the extensions on the non-functional tools, but only Pierrot seemed to do this as an alternative strategy to flipping. However, removing or shortening the lateral extension to make the tool functional was a less efficient strategy time-wise than flipping the tool.

Rapid learning is probably highly advantageous for opportunistic generalists like corvids to quickly take advantage of short-term resources (Goodwin 1986). Rooks, for example, are reported to have solved a modified trap-tube problem quicker than most primates in related studies (Seed et al. 2006). There were four possible cases of rapid learning in my experiments. (i) Pandora (for which the order of experiments was 1, 3, 2) never once flipped a pandanus tool in Experiment 1 but flipped non-functional sticks in blocks 5 and 6 of Experiment 3. In Experiment 2 she unexpectedly flipped one barbless pandanus tool three times. Given that the appropriate end of the stick tool to use was probably easier to detect, she may have learned to flip the stick tool in the course of the experiment and then applied that knowledge to a non-functional pandanus tool. (ii) Brando only began flipping the non-functional pandanus tool in trial 6 after either giving up or getting a replacement tool in the first five trails. He then flipped the tool in all the subsequent barbs-down trials. (iii) Max may have learnt to flip pandanus tools in the first two blocks of Experiment 1 because his latencies to flipping decreased noticeably over these trials. Furthermore, after not flipping the functional tool in the last six trials of blocks 3 and 4, he immediately resumed flipping the non-functional tool in block 5. He appeared to have rapidly obtained information about the tool itself (i.e. barb direction) or feedback from the way it operated to suggest that it was non-functional. His performance in Experiment 2 suggested that the latter explanation was the more likely one. (iv) The continued flipping of functional tools in block 3 of Experiment 1 suggested that the crows had developed a pattern of automatically flipping tools because of previous experience in blocks 1 and 2. However, the reduced flipping in block 4 compared to block 3 suggested that crows quickly learnt that it was not necessary to flip the functional tool.

Overall, my results suggest that the crows pay little attention to the barbs on pandanus tools. Instead, they appeared to respond to non-functional tools in the tasks that I set by using one or a combination of three strategies: (i) flip it, (ii) replace it, or (iii) modify it. I suggest that successful pandanus tool use in the wild relies heavily on procedural knowledge about the sequence of operations required to make a successful pandanus tool.

Supplemental Data: Video 4.1 is available in the supplementary data CD included in this thesis and at http://dx.doi.org/10.1007/s10071-007-0108-1. For caption, see Appendix, p. 137.

5 Conclusions

Approximately 3500 hours of fieldwork that I conducted on New Caledonian crows on Maré have gone a substantial way to answer some of the fundamental ‘unknowns’ – the social structure of NC crows, the ontogeny of their pandanus tool skills, and their understanding of tool related folk physics – addressed in the introduction of this thesis. The approach of setting up feeding tables with attached pandanus trees in the crows’ natural habitat provided me with a unique opportunity to observe their behaviour in a largely naturalistic setting, while at the same time making my observations reproducible and standardised. My observations did not disturb the crows’ daily routines or interfere with their family relationships, and I believe that my results generally allow immediate transfer to crows’ ‘wild’ behaviour. A recent study investigating NC crows’ stick tool use at natural foraging sites on Grande Terre (Bluff et al., 2010) yielded similar results regarding juveniles’ opportunity to use discarded tools and observe parental tool use, which confirms the ecological validity of my approach. In this concluding chapter, I describe the picture emerging about NC crows’ sociality, the development of their tool abilities and their grasp of physical properties of their everyday tools.

Sociality

NC crows are ‘typical crows’ that live in stable, monogamous and possibly lifelong relationships with their partner with whom they travel year round. In general, the female incubates and broods the eggs, while both partners feed the juveniles before and after fledging. On a social scale, NC crows appear at the lower end of corvid sociality. Their core unit is the immediate family, consisting of two adult partners and their offspring from up to two consecutive years. Although juveniles delay dispersal for up to 20 months and may be fed by both parents throughout this time, I have found no indication of communal breeding or helpers at the nest. By the end of their first year the juveniles' learning about the technical aspects of tool manufacture is largely completed and they appear to be nutritionally independent. In Chapter 2 I therefore propose that the main reason why juveniles further delay dispersal is to profit from a 'safe haven' (Ekman & Griesser 2002) provided by the parents, allowing them to optimise their foraging skills in an environment of reduced predation threat and intra-specific competition. The disposition of adult males' to tolerate other crows at valuable food sources like our feeding tables suggests that the social network size of crows on Maré does not exceed 16 individuals, including up to five immediate family members. The foraging areas of different families overlap considerably, and I have found no obvious signs of territorial behaviour.

Development of Tool Manufacture and Tool Use

The results of my developmental study (Chapter 3) show that, contrary to the results of Kenward et al. (2005, 2006), the development of proficient pandanus tool manufacture and use is a very extended process, comparable to that in both human and non-human primates, and that social learning appears to play an important role. Before acquiring adult-like technical proficiency at about 10-12 months of age, juveniles go through different stages of non-proficient pandanus tool manufacture. Uncoordinated ripping at pandanus leaves that may result in the removal of usable parts is followed by more coordinated sequences. However, even coordinated ripping does not necessarily result in a functional tool because of mistakes in the manufacture process, like non-aligning rips or an incorrect order of rips which renders a tool non-functional if not turned around. Only towards the end of their first year are crows able to reliably manufacture functional pandanus tools, and adult manufacture speed is only reached several months later. Correct tool using techniques develop faster (after around seven months), but are also preceded by a period of incorrect usage through faulty probing, and juveniles do not reach adult extraction speed before the age of at least 12 months.

One important mechanism by which juvenile crows learn to manufacture and use pandanus tools appears to be individual trial and error learning. However, this takes place in an environment that is strongly scaffolded by their parents. By following their parents, juveniles are led to pandanus trees, which may promote tool related behaviours via local enhancement. They may also profit from their parents' tool manufacture and use in several other ways.

1) Young crows in their first six months are fed large parts of the food their parents extract and are allowed to scrounge frequently. Since the young crows are generally not rewarded by their own efforts during the first 3-6 months, this is likely to keep them motivated to use and manufacture tools. Moreover, the possibility to scrounge from conspecifics is likely to facilitate social learning in birds and primates (Midford et al. 2000; Caldwell & Whiten 2003).

2) Juveniles do not only scrounge meat, but also frequently use tools left by other individuals, both before and after they use their first own tools. Given the close proximity and the considerable amount of time juveniles spend with their parents during their first half year, they are probably much more likely to use their parents' tools than those of non-related crows. Similar to the benefits of scrounging food, the use of tools formerly used or manufactured by experienced conspecifics is likely to support proficiency in naïve individuals (Hirata & Morimura 2000; Hirata & Celli 2003).

3) Counterparts that remain on pandanus trees after parental tool manufacture appear to facilitate the early development of juvenile tool manufacture by providing easily accessible ‘starting points’ for manufacture. They might also guide juveniles in respect to the suitable position to make a first rip along the leaf edge, and to the correct depth of a rip.

4) Juveniles have ample opportunity to observe both tool manufacture and use from a close distance. While juveniles appeared to pay little attention to tool manufacture at the feeding tables, this might be partly due to the artificial spatial separation between tool manufacture and subsequent tool use created by the set-up of the feeding table. In a pandanus tree away from feeding tables, the locations of tool manufacture and food extraction are usually only a few centimetres apart. A juvenile watching tool use will therefore very likely have watched the manufacture as well. My results in Chapter 3 show that crows on Maré manufacture pandanus tools using slightly different manufacture variants, and that certain variants are dominant within families. This is consistent with the idea that juveniles copy the variants that they see their parents use. However, the differences between those variants are subtle and different variants were only analysed in detail for two families. I can therefore not exclude the possibility that each crow discovers different variants by itself, and that the correspondence within the two families is due to chance.

Because the evidence for imitation of tool manufacture techniques is only tentative, I have suggested an alternative mechanism that could enable the faithful transmission of tool designs even in the absence of high-level social learning like imitation: template matching. Through the use of discarded parental tools and counterparts juveniles might form a mental template of functional tool design, to which they gradually match their own tool manufacture.

Implications for Understanding Tool Use by Crows on Grande Terre

How can the findings on crow sociality and development of wide tool manufacture on Maré contribute to explain the existence and geographical distribution of different tool designs on the mainland of New Caledonia? Hunt & Gray (2003) have suggested that the more complex multi-stepped tools have evolved through cumulative improvements to the more basic wide design. That is, the stepped design was selected for because of superior tool properties (a sturdier holding end and a longer, more flexible probing end than in uniformly wide tools). This would explain why it is by far the most common design with the widest geographical distribution. An important requirement for this scenario is the faithful social transmission of tool designs. In particular, vertical transmission (i.e. from parents to offspring) appears suitable for creating a ratchet effect to maintain individual improvements un-diffused by horizontal transmission (Sterelny 2006).

The social organisation of NC crows on Maré also appears suitable for promoting cumulative technological evolution. The crows' clear preference to interact with family members and only rarely share rich food sources (like feeding tables and, presumably, un-observed pandanus trees) with non-related individuals is likely to strongly favour the vertical transmission of information and inhibit horizontal transmission (i.e. between non-related individuals). Juveniles are therefore much more likely to learn from their parents (and also older siblings who have previously learned from the same parents) than to adopt manufacture styles from outside the family.

The extended period of parental care, in particular the close association between parents and juveniles during the first six months of life, are also likely to help maintain design characteristics within families and minimise the influence from 'outside'. While the duration of post-fledging care in cooperatively breeding birds is often extended (Caffrey

1992; Langen 1999; Clayton & Emery 2007), juveniles from non-cooperatively breeding species are often independent after only two to three months post fledging (Langen 1996; Russell 2000; Kaplan 2004). On Maré, juvenile NC crows spent up to 40% of their time at tables with at least one parent during their first six months. Even if non-related birds were present, the juveniles were likely to be much closer to their parents than to the non-family individuals. The developmental pattern of tool manufacture that I found in Chapter 3 suggests a sensitive learning phase within the first 3-6 months. After this time, tool manufacture techniques are largely adult-like and juveniles have settled on one main manufacture variant. Juveniles are then probably less likely to adopt different strategies from other crows. This is also true if the mechanism of transmission is not copying of motor patterns but template matching. By following their parents closely, juveniles are more likely to use tools discarded by them or start manufacture at counterparts the parents have just produced, than profit from the products of other birds. More generally, extended parental care obviously positively affects juveniles' opportunities for social learning by direct observation.

Could the mechanisms observed on Maré allow for high fidelity social transmission? Theoretically, yes. While the methodological approach I used does not allow me to distinguish between the exact mechanisms of observational learning like imitation or emulation, young crows clearly have ample opportunity to watch tool manufacture and use from close quarters. My results show that the bulk of juvenile crows' learning is likely to be individual trial and error, which is probably crucial for gaining knowledge about the physical properties of their tools (Lockman 2000). At the same time, that does not necessarily prevent them from learning important details of the manufacture process via direct observational learning. However, the exact mechanisms by which high fidelity social transmission occurs might not be crucial to evolve the different material cultures described by Hunt and Gray (2003). As Heyes (1993) pointed out, the processes that support culture are not necessarily defined by the mechanism of transmission, but are those that "...insulate socially transmitted information from modification through individual learning." (p. 1006). One of these processes might include the storage of information in artefactual material (Heyes 1993) – like discarded tools and counterparts that might be used as templates.

Remaining Issues Concerning Tool Manufacture

While observations of wide tool-making crows on Maré enable us to answer many of the questions regarding NC crows and their tools, several issues concerning the behaviour of these crows on Grande Terre remain to be investigated.

First, is the social life of crows on Maré the same as that on Grande Terre? One major difference between these populations is their density. Crows are extremely abundant on Maré (much to the dislike of many local farmers whose crops they eat), whereas their density on Grande Terre is much lower in areas where pandanus tools are made (G.R. Hunt, personal communication). However, a lower density is unlikely to influence the crows' principal social organisation, i.e. life in small family groups. If anything, a lower population density should promote vertical transmission even more, and would therefore not compromise the faithful transmission of tool designs. Juveniles on Maré delay dispersal for an extremely long period, and it is reasonable to assume that they do so on Grande Terre as well. However, we are largely ignorant about what happens after juveniles leave the close company of their natal family. The juvenile that I have observed the longest, Brando, began pairing up with an adult female about three months after he was last observed being fed by his parents. The new pair visited feeding tables together for three months before suddenly disappearing. Because the female had been a breeding resident of the study area for at least a year, it seems unlikely that the couple moved to a different area; they might have been victims to shooting or predation. Two more juveniles, Orange and Primo, both disappeared at around 20 months of age, while another individual, Abel, was visiting feeding tables with a partner and two dependent chicks in late 2008, when he was nearly 2 years old. Therefore, both dispersing from and staying in the parental foraging area after independence appears to be a possible strategy. However, dispersal dynamics have clear implications for the spread and geographical distribution of tool designs and should therefore be investigated in greater detail.

Second, the cumulative technological evolution via high fidelity social transmission as suggested by Hunt and Gray (2003) implies that each individual crow and, in fact, each individual family, only manufactures one of the three tool designs. However, we do not know if this is the case. In Parque Rivière Bleue on Grande Terre, wide, narrow and stepped tool designs occur at the same site and can even be found on the same pandanus tree (Hunt & Gray 2003; G.R. Hunt personal communication). A ‘one-crow/one-tool’ system should be confirmed before further speculation on the transmission and development of tool designs is made.

This leads directly to two more issues related to tool design: the properties of the different designs, and the apparent lack of ecological correlates. Stepped tools appear to combine the benefits of both wide and narrow tools: they provide a sturdy holding end, while at the same time having a long and flexible working tip, suggesting greater foraging efficiency. Tests with human experimenters showed that chimpanzees’ brush-tipped probing tools are more efficient at termite fishing than unmodified tools (Sanz et al. 2009).

Similarly, experimental work could clarify whether stepped tools are really more efficient in extracting prey than the two simpler designs.

The lack of ecological correlates accounting for the differences between the three pandanus tool designs is one important argument in favour of the cumulative technological evolution suggested by Hunt and Gray (2003). However, ecological variables associated with the designs were never examined directly. One of the flagship examples of chimpanzee culture, ant dipping (McGrew 1974; Boesch & Boesch 1990), has been undermined by recent investigations. These studies link differences in the length of anting tools and the way chimpanzees eat ants to differences in speed and aggressiveness of the ant species that are being harvested, rather than to cultural factors (Humle & Matsuzawa 2002; Humle 2006). Several authors therefore challenge the claim that differences in anting tools and other cultural traditions are caused by cultural, rather than ecological, factors (Möbius et al. 2008; Schöning et al. 2008; Tennie et al. 2009). Future work on NC crows should investigate possible ecological factors (such as living habits of closely related prey species) that might have contributed to the evolution of the different pandanus tool designs on Grande Terre.

Most importantly, we need to directly investigate the ontogeny of stepped tool manufacture. My observations on Maré suggest that different kinds of social learning play an important role in the individual development of wide tool manufacture. However, wide tools are fairly simple to manufacture. The strong parallel fibres of pandanus leaves ensure the production of a uniformly wide strip of material, once a crow has cut into a leaf edge and starts ripping. As Kenward et al. (2005) have shown, naïve crows can produce roughly made strips of pandanus leaves suitable for meat extraction without social input. While it is therefore possible that naïve juveniles could develop adult-like wide tool manufacture by individual trial and error learning alone, this is hard to imagine with the much more complicated process of stepped tool manufacture. The only way to obtain a conclusive picture of the processes involved in stepped tool manufacture is to observe stepped tool manufacture in the wild and/or in captivity.

Folk Physics

Given the remarkable tool manufacture skills of NC crows and their ability to successfully exploit functional aspects (like length and diameter) of tools demonstrated in laboratory (Chappell & Kacelnik 2002, 2004; Weir et al. 2002) and field experiments (Hunt et al. 2006), I would have expected them to ‘understand’ the basic functional feature of one of their most common tools: the barbs along the edge of pandanus tools. Somewhat surprisingly, this did not seem to be the case. Their behaviour when presented with tools where the barbs were either lacking or incorrectly orientated suggested that they did not pay attention to either the existence or the direction of the barbs. Rather, the crows appeared to respond to non-functional tools by applying one or more of three associative strategies: flip it, replace it, or modify it. At the end of Chapter 4 I suggested that successful pandanus tool use relies heavily on the appropriate procedural knowledge to make a functional pandanus tool. The developmental study (Chapter 3) clearly supports this suggestion. The stages of tool manufacture juveniles pass through during their ontogeny suggest a gradual accumulation of ‘knowledge’ about how to manufacture a useful tool. During that process, juveniles were frequently observed to flip, attempt to modify, or discard non-functional pieces of pandanus leaves that they had ripped off the tree (JCH unpublished data). By optimising the manufacture process individuals ensured that they eventually always end up with a functional tool. It might therefore simply not be necessary for NC crows to pay attention to the barbs.

Still, the result that the crows do not attribute importance to the most prominent and important feature of the tools they use many times each day is somewhat at odds with the sophisticated cognitive abilities they have recently shown in the aviary experiments conducted by Taylor and colleagues. Experimentally naïve crows from the same population that provided the individuals for my studies were able to spontaneously solve a meta-tool task (Taylor et al. 2007), and could solve a spatial analogy problem that human children only succeed at from 3.5 years of age (Taylor 2009). Moreover, the crows responded to the trap tube task in a way that suggested they were able to identify and learn about causal interactions (e.g. ‘avoid pulling meat behind a hole only if the hole is in a functional position’) (Taylor et al. 2009a, b). Unlike chimpanzees (Martin-Ordas et al. 2008), NC crows were also capable of transferring this rule to a perceptually different setup, the trap-table (Taylor et al. 2009a). Additionally, in a series of experiments conducted by Wimpenny et al. (2009), long-term captive NC crows (including two hand-raised individuals) could use up to three tools sequentially to achieve a final goal, a capacity not shown in any other non-human species. Why do crows that are so smart not appear to realise that the barbs on their tools are important?

In general, differences between a species’ abilities and performances in the wild and those in captivity are not uncommon. For example, a number of species that never – or only very rarely – use tools in the wild can learn to do so in captivity (for example, baboons *Papio hamadryas*: Beck 1972; gorillas: Boysen et al. 1999; Parker et al. 1999; cotton-top tamarins: Hauser et al. 2002; Santos et al. 2005, 2006; rooks: Bird & Emery 2009). Chimpanzees and capuchin monkeys are accomplished tool users in the wild

(Whiten et al. 1999; Ottoni & Izar 2008), but their comprehension of tools appears limited to perceptually salient features rather than causal understanding or functional properties (Visalberghi & Trinca 1989; Visalberghi & Limongelli 1994; Povinelli 2000).

Explanations given for these differences between wild and captive performances are mostly rather vague. Weiss et al. (2005) hypothesise that while cotton-top tamarins are capable of planning ahead, the scope of their planning might be too limited to allow tool use in the wild. Santos et al. (2006) suggest that individuals might not be able to fully employ their knowledge when confronted with real world problems. According to Müller (2009), animals in the wild may 'get by' with cognitively more simple strategies than sometimes suggested by captive studies. Similarly, a possible explanation for the failure of NC crows to reliably attend to barbs on pandanus tools might be 'why think if I don't have to?'

Hunt and Gray (2003) suggested a plausible scenario for the initial development of pandanus tool manufacture and use. NC crows often rip wide strips of leaf edges towards the trunk of a pandanus tree to gain access to prey hidden in the crevices between emerging leaves. These strips generally remain hanging from the leaves and are not used as tools. However, the ripping may have easily led crows to removing strips and using them as tools. Under this scenario, fast learning abilities, curiosity, flexibility and inventiveness might have been sufficient to develop tool manufacture in the absence of causal understanding about physical properties of the materials involved. In fact, studies investigating stick tool use in NC crows suggest that the evolution of motivational mechanisms, rather than cognitive abilities, might have been the driving force behind the development of tool use (Kenward et al. 2006; Kacelnik 2009; Bluff et al. 2010). In an environment where the best food (e.g. slugs and grubs) is hidden in deep leaf crevices and narrow holes in dead trees, a high motivation to poke, probe, insert objects and search for hidden food might certainly be adaptive. The willingness of the juveniles in my developmental study to persistently rip at pandanus leaves and probe for many months without frequent nutritional reinforcement supports this idea.

On the other hand, during their ontogeny to accomplished tool manufacturers young crows clearly learn a lot about the properties of the materials involved, such as flexibility, thickness, tearing properties, etc. It might therefore be argued that NC crows do not use tools because they are smart, but that they are smart because they use tools. This is, in short, the claim of the technical intelligence hypothesis. Experimental work by members of the University of Auckland crow research group is currently underway to explore this possibility by comparative studies between closely related corvid species that differ in their tool using abilities.

Conclusion

When I started this thesis, I set out to answer some of the many ‘unknowns’ that are essential to explain New Caledonian crows’ remarkable tool skills, their development and geographical patterns. I investigated NC crows’ social structure, the development of their pandanus tool skills and their grasp of tool related folk physics. While some of my results confirmed previous suggestions, others were rather surprising. The social life of NC crows on Maré fully confirmed the preliminary observations by Hunt (2000b) and Kenward et al. (2004) and fit well into the mechanisms suggested to explain the tool patterns observed on Grande Terre by Hunt and Gray (2003). The results of the developmental study are clearly at odds with Kenward et al.’s (2005, 2006) observation of the rapid development of tool skills, and agree with Hunt and Gray’s (2003) suggestion that social learning plays an important role in the ontogeny of tool manufacture. However, the exact mechanisms that might lead to the faithful transmission of tool designs are still unclear. As an alternative mechanism to imitation, for which the evidence is only tentative, I suggest template matching. Experimental work is necessary to investigate this possibility. Likewise, observations of wide tool manufacture can only go so far in attempting to explain the development of stepped tool manufacture, and fieldwork on Grande Terre is needed to gain a more complete picture. Finally, the results of the experiments regarding folk physics were surprising because they suggest only limited understanding of the physical aspects of the tools the crows use in everyday life. The picture emerging from both field and laboratory work is one of intermediate cognition in NC crows. My work also emphasises the importance of both approaches to obtain a complete picture of a species' abilities and the scope in which they are realised in 'real life'. At the end, there are still many 'unknowns' to be answered. Will we ever really unravel the mysterious minds and abilities of these remarkable birds?

Quoth the raven: Nevermore!

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Appendix 1

A data CD is included in the folder bound inside this thesis. It contains the following folders and sub-folders:

Electronic thesis: this thesis itself in pdf format

Video footage:

Chapter 3: Development of Tool Manufacture and Use in New Caledonian Crows

Video 3.1: Development of proficient pandanus tool use in baited logs

This video shows proficient pandanus tool use by an adult male and three different faulty probing techniques (defined in Table 3.2, p. 48) used by juveniles during their ontogeny to proficient pandanus tool users.

Clip 1: Adam extracts a piece of meat from a baited log at a feeding table. He then feeds the meat to Cain (ca 5 months old), who has been watching the extraction.

Clip 2: Wrong angle probing: Primo (ca. 2 months old). He tries to insert a tool into a hole but fails because he holds the tool at a wrong angle (note that Primo is using a tool that has just been dropped by his mother Pandora).

Clip 3: Folding: Primo (ca. 4 months old) takes a tool that is already in a hole and twists and bends it without actually probing.

Clip 4: Defective probing: Abel (ca. 4 months old) inserts a tool with both ends pointing upwards out of the hole and then probes.

Video 3.2: Juveniles' pandanus tool manufacture techniques

This video shows the five different techniques of tool manufacture (defined in Table 3.2, p. 48) used by juveniles during their ontogeny to proficient pandanus tool manufacturers.

Clip 1: Technique 0: Abel (ca. 4 months old) rips in a non coordinated fashion at a pandanus leaf hanging onto the feeding table, but does not manage to remove a tool.

Clip 2: Technique 1: Primo (ca. 5 months old) removes a piece of leaf by ripping uncoordinatedly at a pandanus leaf. Note that in Techniques 0 and 1 the birds start their ripping at a damaged leaf edge.

Clip 3: Technique 2: Bo (ca. 8 months old) attempts to manufacture a tool with a coordinated cut-rip/cut-rip action. Because the second action cuts into the leaf more deeply than the first one, the rips do not align and the tool cannot be removed from the leaf.

Clip 4: Technique 3: Primo (ca. 8 months old) manufactures a tool using a coordinated cut-rip/cut-rip action. However, because the second cut-rip starts closer to the leaf base than the first one, Primo removes the tool holding it with the barbs pointing downwards.

Clip 5: Technique 4: Primo (ca. 18 months old) proficiently manufactures a pandanus tool, and uses it to extract meat from a baited pandanus tree.

Video 3.3: The three variants of adult-like pandanus tool manufacture

This video shows the three different variants of pandanus tool manufacture (Figure 3.6, p. 59) which may occur whenever a crow manufactures a tool with coordinated cut/rip actions. For better visibility, all tool manufactures are shown at one third of the original speed.

Clip 1: Variant A is used by all birds to a certain extent. Adam manufactures a pandanus tool with two cut-rip actions that join about half way along the tool.

Clip 2: Variant B was predominantly used by families 1 and 2 (Pandora, Abraxas, Primo and Yor). Abraxas makes a cut that is followed by a rather long rip. The second cut removes the tool from the leaf without ripping towards the first cut-rip.

Clip 3: Variant C was mainly used by Family 3 (Cain and Abel). Cain (ca. 9 months old) makes an initial cut, then a long cut-rip that joins the first cut.

Chapter 4: Do New Caledonian Crows Attend to the Properties of their Tools?

Video 4.1: Experiment 1 (tool flipping), Brando, Trial 10

This video shows an example of a crow flipping a pandanus tool. A pandanus tool is presented barbs-down (non-functional). Brando probes with the barbs-down tool for about four seconds, then flips it and extracts the meat. The flip is played at half speed for better visibility.