ECOLOGICAL, MORPHOLOGICAL AND BEHAVIOURAL ASPECTS OF TOOL-USE IN NEW CALEDONIAN CROWS

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A thesis submitted to

The University of Birmingham

for the degree of

DOCTOR OF PHILOSOPHY

School of Biosciences

College of Life & Environmental Sciences

University of Birmingham

September 2011

Abstract

New Caledonian crows are amongst the most sophisticated tool-users in the animal kingdom. In this thesis I present my findings from various aspects of the crows' behavioural ecology, morphology and cognition, contributing to our understanding of how this fascinating tool-use behaviour might have evolved. My studies in the field reveal new types of tool manufacture and foraging behaviour that help to build up a complete picture of the ecological importance of tool-use to wild crows. Additionally I demonstrate the subtlety and skill required to extract wood boring beetle larvae from their burrows, accounting for the slow development of tool-use proficiency in juvenile crows. Further work reveals how their unique visual field combines with a peculiarly straight bill to facilitate tool-use; perhaps the only evidence outside of the hominid hand for tool-use specific morphology. Recent studies suggest *Corvus* species are behaviourally and cognitively predisposed to become tool-users, however, through multiple lines of enquiry this thesis highlights the costs that New Caledonian crows bear in order to become successful tool-users. The unique ecological conditions in New Caledonia are likely to have made this costly form of foraging possible, helping to explain why tool-use is so rarely observed in other animals.

Acknowledgments

First and foremost I would like to thank Jackie; I could scarcely have hoped for such a supportive, helpful and friendly supervisor to guide me through my PhD. I wish to thank Christian for his crucial guidance and attention to detail and I am indebted to Graham, whose endless enthusiasm and help was a great source of inspiration. Huge thanks to Lucas, not only for considerable help and technological expertise, but also for preserving my sanity through the long hours of fieldwork. Augusta provided kind help in the lab and field, and vital access to crows and contacts, but I am also enormously grateful for her wonderful hospitality in Leutstetten.

Many thanks to Serge Blancher, who was not only instrumental in facilitating our fieldwork, but whose incredibly kind family welcomed me to their Christmas celebrations for three years running. Thanks to Bob for his hospitality and logistical help, and enlightening me with many new foods and hunting practices. Thanks to Jacques and his family for all their hospitality, fish, deer and help chopping down trees, and to Steve for his instrumental help rescuing the car I managed to sink. Many thanks to Eleanor for a friendly place to stay in Noumea, and to Danika for help in the field. Thanks to Jo Cooper and everyone at The Natural History Museum at Tring for allowing me access to skins and skulls. Many thanks to Mark Edge and Michelle Pitt for allowing me access to their corvids. Also thanks to Thomas Bugnyar, Claudia Wascher and Anna Braun at the Konrad Lorenz field station in Grünau for access to their ravens. Thanks to the authorities in New Caledonia who permitted my fieldwork, and who were kind enough to provide us with free accommodation, and to the tribes who allowed us to work on their land. I am very grateful to the BBSRC and British taxpayers for funding my PhD.

Emma has provided incalculable emotional support through my PhD, but also made for an excellent assistant during visual field work. Thanks to Simone for all her statistics help and to all in W108 and W107 for creating a great place to work.

Without my excessively academic family's passion for science and continued support I would probably never have pursued such an odd career, so many thanks to Sue, Tom, Adam and Emily.

I wish to thank Gavin Hunt for bringing the New Caledonian crows' fascinating behaviour to the attention of the scientific community, and to the rest of the Auckland team for their substantial and stimulating contributions to our competitive field.

Finally, I would like to thank Uek, Corbeau, Betty and all the other captive and wild New Caledonian crows, corvids and parrots that have put up with my incessant experiments and tolerated the various bits of equipment I've strapped to them.

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Contributions of Collaborators & Supervisors

Unless stated otherwise this thesis was first drafted by JT with comments and minor edits provided by JC. All figures were prepared by JT with input from JC & CR.

Chapter contributions:

2) The grass-stem tool manufacture observation was based on a paper; drafted by JT and co-written by LAB & CR.

3) The use of crow-borne video cameras was conceived by CR, who also led the development of second-generation solid-state video loggers. Camera control boards were designed and built by Ron Joyce, in collaboration with CR. All logger units were assembled and programmed by JT with timer schedules designed by JT and CR. Crows were trapped by JT and CR with assistance from AB, and cameras were recovered by JT and CR. JT scored all video footage and analysed the data.

4) The larva-cam concept was conceived by JC and JT. Larva-cam units were designed and built by JT, experiments were designed by JT, JC, CR, and LAB, and data were collected in the field by JT with support from CR and LAB. Analyses were performed by JT with input from CR and JC.

6) Visual field mapping was conceived by JT, JC, CR and GRM. All data were collected by JT following training in the ophthalmoscopic technique provided by GRM with

logistical support from AB, CR and Emma Rosenfeld. Statistical analyses were performed by JT with further suggestions from Philip Cassey and Simone Webber.

7) The ophthalmoscopic filming tool-use experiment was conceived and designed by JT. The apparatus was designed and built by JT. Data were collected by JT with logistical support from CR. Statistical analyses were performed by JT.

8) Bill morphology for tool-use analysis was devised by JT, JC and GRM. Data were collected by JT with help from three blind volunteers. Statistics were performed by JT.

10) The see-saw paradigm was conceived by JT. The apparatus was designed and built by JT, and all data were collected by JT, with support in New Caledonia from CR.

11) The string pulling experiment was conceived by CR. Data were collected by JT with logistical support from CR.

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0.1 Preface

Tool-use is one of the most notable characteristics of human existence; almost every aspect of our modern lives depends on tools that have been developed over thousands of years. Until comparatively recently humans were thought to be the only sophisticated tool-users in the animal kingdom (e.g. Goodall, 1970), so observations of non-humans using tools in the wild called into question our unique status and provided a new line of comparative research for investigating what makes humans unique and how we might have evolved these abilities. Throughout the 20th century the bulk of tool-use research focussed on our closest ancestors, such as the chimpanzee (*Pan troglodytes*), whose tool-use abilities are likely to have been shared with our last common ancestor. But while tool-use is rare throughout the animal kingdom, it has been documented in a number of species that are evolutionarily distant from primates (Beck, 1980). These species allow us to investigate traits and abilities associated with tool-use that have evolved in parallel with our own, and as such can highlight common constraints or pressures that might shed light on early human evolution.

Endemic to an island in the south Pacific, the New Caledonian crow *Corvus moneduloides* is one of the most sophisticated tool-users in the animal kingdom. My aim in this thesis is to investigate how and why tool-use evolved to such a remarkable degree in New Caledonian crows (‘NC crows’ or ‘crows’ hereafter), contributing to our understanding of how tool-use can evolve in parallel to humans. There are a number of possible lines of investigation to such a question because many different factors are likely to play a role, from the ontogenetic and social learning mechanisms that might propagate tool-use behaviour, to the unusual ecological conditions that promoted it. Although NC crows have been studied for 15 years there are many unanswered questions, from their basic ecology to their cognitive abilities. In the first Part of my thesis I consider the behavioural ecology of NC crows, reviewing what we already know and providing evidence from data collected in the wild. This research suggested new lines of investigation into potential morphological specialisations for tool-use in NC crows which I present in the second Part of the thesis before finally considering the potential importance of cognitive adaptations for tool-use, a field of research that has attracted considerable interest in recent years. While these different facets of NC crow ecology and behaviour are all involved in the evolution of their tool-use behaviour, each draws from quite distinct areas of research. I therefore review the relevant literature before each of the three thesis Parts, rather than presenting a single introduction spanning numerous disciplines.

1 PART ONE – BEHAVIOURAL ECOLOGY

1.1 New Caledonia's Natural History

The geological history of New Caledonia has dramatically influenced the island's florae and faunae, resulting in unique ecological conditions that are likely to have played a key role in the evolution of tool-use in its endemic crows. I shall briefly review some relevant aspects of the island's history that help to explain how this situation developed before assessing the behavioural ecology of New Caledonian crows.

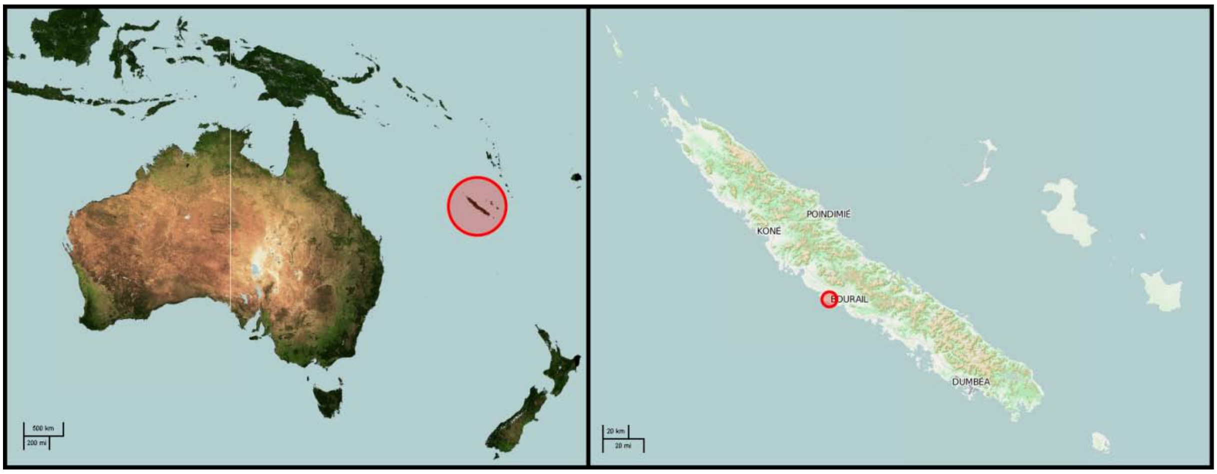

Figure 1-1. Map of the South Pacific with New Caledonia highlighted in red (left panel), and a map of New Caledonia with the location of our field site highlighted in red (right panel). Source – openstreetmap.org.

Grande Terre is a cigar-shaped island *c*. 450km long and *c*. 50km wide, with a mountain range running along its length reaching altitudes of more than 1600m (see Figure 1-1). Humid, tropical forest covers the highland and east coast, while dry forest and anthropogenic savannah lines the west. Ultrabasic soils in the south, rich in nickel, cobalt and copper, support almost entirely endemic and apparently ancient plant ecosystems where mining has yet to devastate them. Coral atolls raised from the sea nearby have created the Isle of Pines to the south-east and the Loyalty islands to the east, which only reach altitudes of 262m and 138m respectively. Together, these islands make up New Caledonia, situated on the Norfolk Ridge along with New Zealand approximately 1700km to the south and Norfolk Island half way between. Grande Terre is a small piece of the mostly submerged continent of Zealandia, a fragment of continental crust that broke free from the Gondwana supercontinent; first parting with Antarctica between 85-130 Ma (million years ago), and then Australia *c*. 65-83 Ma (Grandcolas et al., 2008; Sharma & Giribet, 2009). There appears to be consensus amongst geologists that Grande Terre was then submerged deep in the ocean from *c*. 65 Ma, emerging just *c*. 30 Ma; this is supported by the distribution of marine limestone sedimentation and fine-grained black chert that only forms under high pressure. Such prolonged submersion is at considerable odds with the biotic evidence. The high levels of endemism and unique florae and faunae of New Caledonia are thought to have derived directly from Gondwana, but with no known land-bridges to nearby islands or continents to support recolonisation, and with deep submersion of even the highest mountain peaks on Grande Terre, this has created quite a conundrum. Many of the unique species on New Caledonia can be attributed to recent dispersal from other land masses, rather than ancient Gondwanan origin (Grandcolas et al., 2008). However, the existence of a few endemic relict species, such as the oldest extant sister of the flowering plants, *Amborella trichopoda*, or the flightless bird, the kagu *Rhynochetos jubatus* cast doubt on this theory. Perhaps the best evidence for the continuity of the New Caledonian biota comes from the endemic harvestman family Troglosironidae (Opiliones: Cyphophthalmi); a group of species exceptionally poor at moving between islands, making them ideal for island biogeographical studies. Molecular evidence shows that this group diversified from its sister groups in South America and West Africa a long time ago (124-246 Ma), persisting through the 'Paleocene drowning' of New Caledonia, but presumably suffering catastrophic extinction given their subsequent diversification only *c*. 49 Ma (Boyer & Giribet, 2007; Sharma & Giribet, 2009).

The Corvidae are thought to have diversified from the Passerines in Australia and Papua New Guinea while New Caledonia was submerged (Sibley & Ahlquist, 1990; Boles, 1995; Barker et al., 2002; Ericson et al., 2002). The only Passerines thought to have split from Gondwana on the Zealandia continent are the New Zealand wrens, which are basal to the oscine/suboscine divergence (Hackett et al., 2008). This means the NC crows' ancestors must have colonised Grande Terre from elsewhere, but there is no geological evidence for land bridges to New Caledonia that could date their likely arrival, and phylogenetic data for the *Corvus* genus is conspicuously lacking (although a number of groups are currently working on remedying this). As a consequence we currently know very little about the NC crows' closest extant ancestor, or how long ago they are likely to have diverged.

Two notable species groups that missed the Gondwana/Zealandia split and have not made a subsequent crossing are woodpeckers and terrestrial mammals (other than domesticated animals, vermin and game introduced c. 3200 to 4700 years ago by humans – see section 1.2). Throughout most of the world wood-boring (xylophagous) insect larvae are extracted by species with morphological specialisations for locating and excavating this otherwise heavily protected prey. Woodpeckers, for example, excavate deadwood with chisel-like bills and use long, barbed tongues to draw prey from burrows (Bock, 1999; Villard & Cuisin, 2004). On isolated islands where woodpeckers are absent some mammals have evolved convergent morphological specialisations to exploit this niche (Cartmill, 1974). Aye-ayes (*Daubentonia madagascariensis*) of Madagascar and the marsupial genus Dactylopsila of New Guinea and Australia both use elongated fingers to locate and extract prey, and powerful incisors to gnaw open the wood (Sterling, 1994; Rawlins & Handasyde, 2002). Evidence for New Caledonia's lack of such extractive specialists is most conspicuous in the larva-infested deadwood of candlenut trees (*Aleurites molucana*; Euphorbiaceae, known locally as 'bancoulier' trees). While the endemic Cerambycid beetle larvae can live in a number of host trees (pers. obs.), the candlenut is clearly prone to major infestations that can reduce a healthy tree to a honeycomb of deadwood in a few years (Figure 1-2).

Figure 1-2. An NC crow probing for Cerambycid larvae in a heavily decayed candlenut tree trunk. Ten months after this photo was taken there was little evidence of the trees' existence at the same location.

1.2 The Discovery of Tool-Use in New Caledonian Crows

The native Kanak people of New Caledonia have spoken of the industrious tool-use of their local crows for generations (Mariotti, 1996, pers. obs.); but with no reason to think this behaviour peculiar it passed unnoticed by ornithologists and scientists for some time. Only a handful of publications in the 20th century recognised their tool-use behaviour, for example, Le Goupils (1928) provides a second hand report of an observation made in 1909, and Orenstein (1972) tentatively rediscovers the behaviour based on two brief observations. It was not until the end of the century that the remarkable tool-use abilities of NC crows received mainstream recognition, with Gavin Hunt's observations of complex hook-tool manufacture (Hunt, 1996). These observations revealed a repertoire of two highly standardised tool forms (hooked-stick tools and stepped pandanus tools) that NC crows crafted from raw materials through a series of intermediate steps. Hunt described hooked-stick tool manufacture based on four direct observations; the crows selected branching points in living secondary twigs and snapped them off to leave a hook. They then stripped off the leaves and bark, and worked on the tip to fashion a hook (Figure 1-3a).

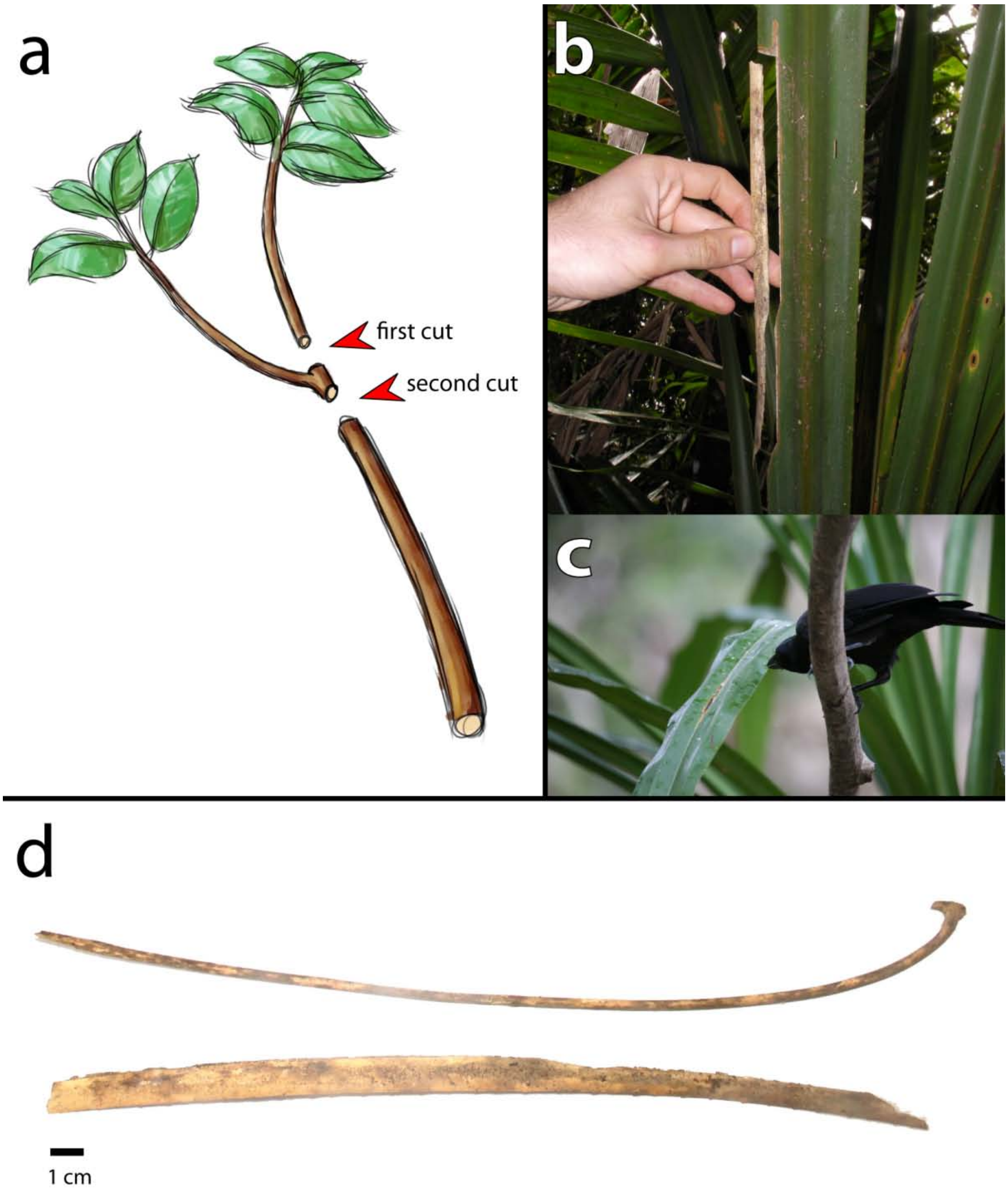

Figure 1-3. a) Illustration of the cuts made by NC crows when manufacturing a hooked stick tool. After making the first and second cuts (arrowed), the crow strips the bark and leaves, and works on the tip to make a small hook. b) A stepped pandanus tool discovered next to its counterpart in the wild. c) A wild NC crow pecking a *Pandanus* spp. leaf. d) An example of a hooked stick tool found inserted into a crevice in deadwood (top) and a stepped pandanus tool found in the crown of a *Pandanus* spp. tree.

Further details of the manufacture process of hooked-stick tools were provided by Hunt & Gray (2004a), who report an adult and its dependent juvenile making 10 tools. They argued that the meticulous sculpting of the hook represented a more advanced form of tool manufacture than that seen in woodpecker finches (variously named as *Cactospiza pallida*, or *Camarhynchus pallidus*; Tebbich et al., 2002; Gill & Wright, 2006 respectively) or chimpanzees (*Pan troglodytes*). However, Pruetz & Bertolani (2007) have since documented savannah chimpanzees producing spears for hunting prosimian prey (bushbabies) hiding in hollow cavities. These chimpanzees apparently crafted their spears using a flexible sequence of steps similar to NC crows' fashioning of hooked-stick tools.

The second major tool-type discovered by Hunt (1996) was made from the barbed leaves of the *Pandanus* spp. tree (Figure 1-3b and c). Based on the counterparts left behind on leaves, Hunt inferred that the crows must have used a series of ripping and tearing steps to form a functional, tapered tool, with a row of sharp barbs acting as hooks. It was a number of years before Hunt & Gray (2004b) observed this manufacture process first-hand; they record a single crow manufacturing and using 'stepped' pandanus tools at a baited log, legitimising the use of counterparts as an artefactual record, and providing additional details on the exact sequence of cuts and tears used by this individual. In contrast to the manufacture of hooked-stick tools by NC crows, brush tools by chimpanzees (Sanz et al., 2009), or termite-fishing tools in Capuchins (Souto et al., 2011), their manufacture requires a number of discrete steps with no functional intermediate forms. Therefore the widespread manufacture of pandanus tools is unlikely to occur through individual learning alone, and must either depend on inherited tool manufacture behaviours, social learning, or a combination of the two (Hunt & Gray, 2003). Pandanus tools are not typically modified after first production – the tool is complete once excised from the leaf (Hunt, 1996; Hunt & Gray, 2004b). This means that the shape of pandanus tools can be reliably inferred from the counterparts that are left behind in leaves after tool removal, and geographical differences in the types of tools made across the island led Hunt & Gray (2003) to suggest that social learning must be used in the development of pandanus tool manufacture (see section 1.3.2).

Subsequent studies added to the list of raw materials used as tools by NC crows (both hooked and non-hooked), such as leaf-stems, bamboo stem, fern stolons, barbed non-native plants, and grass stems (Hunt & Gray, 2002; Hunt & Gray, 2006; Rutz et al., 2007; Hunt, 2008; Troscianko et al., 2008); this flexibility in tool-use and manufacture directed further research to investigate whether NC crows are able to select tools suitable for a given task (see section 9.2.3). Other tool-use modes were also described in the wild; an important example is the use of stick-tools to extract wood boring beetle larvae (*Agrianome fairmairei*; Cerambycidae) from their protected burrows within the deadwood of candlenut trees. Hunt (2000b) observed crows probing for larvae at an artificially provisioned log and describes their ‘fishing’ behaviour whereby crows are thought to aggravate a larva and encourage it to bite onto the tool so that it can be drawn from its burrow (see section 4.1 for further details). New Caledonian crows also eat the ‘candle-nuts’; in order to crack their hard, strong shells NC crows drop them onto rocks (Hunt et al., 2002). However, unlike many other birds which drop shellfish, tortoises or nuts onto rocks (Beck, 1980), the NC crows position the nut on a fork in branches above a regularly used nut-dropping site. Hunt et al. (2002) observed this behaviour at two sites, noting that just 2-3 drops were sufficient to crack the shells. The candlenut tree is therefore thought to play a central role in the tool-use ecology of dry-forest NC crows, leading some to speculate that its introduction by humans could have led to rapid evolution of tool-use in the crows’ recent past (Rutz et al., 2010). Melanesian settlers would have intentionally introduced a number of species to New Caledonia, including the candlenut tree , whose oil-rich nuts were used in candle production (Larrue et al., 2010). The first humans to inhabit New Caledonia were probably people of the Lapita culture, dating back to approximately 3200 years ago (Sand et al., 1998), although there is possibly evidence of pottery pre-dating this by *c*. 1500 years (West, 2009). The candlenut tree is now widespread in the low altitude, dry-forest areas of New Caledonia (pers. obs.), but given this comparatively recent introduction and limited distribution it seems unlikely that NC crow tool-use could have evolved island-wide so rapidly in response to the opportunities provided by this tree alone.

1.3 Tool-Use Development

One of the striking aspects of NC crow tool-use is the apparent ubiquity of the behaviour in most individuals across the entire island – a keen eye can readily spot the tools left behind in burrows, and counterparts left on *Pandanus* sp. trees that evidence the activity. The variety of tool types found in different habitats raises the question of how individual crows adopt tool-use behaviour and the relative importance of nature and nurture in tool-use development. Here I review our current understanding of NC crow tool-use development, providing a background to my studies that investigate the difficulties posed in learning to use tools.

1.3.1 Animal Cultures

Differences in the behavioural repertoires – or traditions – of geographically distinct populations have been discovered in numerous species throughout the animal kingdom (Whiten & Ham, 1992). In the absence of ecological or genetic differences to account for these traditions they are often assumed to be culturally transmitted behaviours. The various definitions of animal ‘culture’ all essentially rely on social learning for the vertical and/or horizontal transmission of information (Boyd & Richerson, 1996; Tomasello, 1999; Laland & Hoppitt, 2003). Examples of such cultural traditions are found in the tool-use, foraging, grooming or courtship behaviours of chimpanzees (Whiten et al., 1999), orangutans *Pongo pygmaeus* (van Schaik et al., 2003), and bottlenose dolphins *Tursiops* sp. (Krutzen et al., 2005). However, it is extremely difficult to prove that behaviours in a natural system are propagated through social learning (Galef & Heyes, 2004), and as such some authors believe cultural traditions have been attributed to social transmission in certain populations based entirely on circumstantial evidence (Laland, 2008). The ecological differences leading to different traditions can be subtle and easily overlooked by fieldworkers. For example, chimpanzees eat army ants *Dorylus* (subgenus *Anomma*) by dipping sticks stripped of bark into an ant column and waiting for them to swarm up. In some areas the chimpanzees sweep their second hand along the tool to collect the biting ants (McGrew, 1974), but in other areas they make shorter tools and draw the ant-covered tool directly through their lips or teeth (Boesch & Boesch, 1990). These different traditions were assumed to depend on social learning alone (Whiten et al., 1999; Whiten, 2001), however, a study has recently found that the ants found in areas where chimpanzees use long tools and first sweep the tool with their hands are faster, more aggressive, and deliver more painful bites than the ants found in areas where the chimpanzees draw them directly into the mouth (Schöning et al., 2008). This highlights the difficulties involved in excluding ecological factors in primate cultural traditions, leading some authors to argue that a greater focus should be directed to non-social aspects of animal cultures, including genetics, asocial learning and ecology (Laland & Hoppitt, 2003; Laland & Janik, 2006; Laland, 2008).

1.3.2 *Pandanus Tool Culture*

Pandanus spp. trees are slow growing screw-pines with long leaves that can remain on the tree for approximately 4 years (Hunt, 2000a); so tool counterparts can provide a faithful record of manufacture stretching back a number of years. Hunt & Gray (2003) collected counterparts from 21 sites across New Caledonia, revealing geographical variation in the types of tools manufactured (Figure 1-4). Tools fell into three obvious shape categories that were classed subjectively: 'wide tools' that are rectangles made from two cuts perpendicular to the leaf and one tear along; 'narrow tools' that are torn from the leaf edge resulting in a far thinner tool than wide tools; and 'stepped tools' that incorporate one or more additional perpendicular cuts to create a tapered tool shape (shown in Figure 1-3b).

Figure 1-4. Distribution of pandanus tool types across New Caledonia (data extracted from Fig. 2 in Hunt & Gray, 2003). Stepped tools are manufactured across the majority of Grande Terre (mainland New Caledonia), however, in the south both wide and narrow tools are produced. On the island of Maré only wide tools were found; NC crows are thought to have been introduced here by humans around 1900 to control crop pests (Hunt, 2000b).

With no obvious ecological factors to account for the geographical variation in the pandanus tool types made by NC crows, Hunt & Gray (2003) suggested this was evidence for cumulative cultural evolution of pandanus tool traditions. However, the tool type distribution is highly significantly correlated with altitude, and I suspect soil type would also show spatial correlation with tool type (soil is ultrabasic in the south, where wide and narrow tools are manufactured). Hunt & Gray dismiss the altitudinal effect, stating that “few” (p.872) ecological variables were found to correlate with tool distribution, even though invertebrate and plant abundance and diversity are known to vary with altitude (Wolda, 1987; Givnish, 1999): “Variation in the raw material, altitude and rainfall does not appear to be a significant causal factor of the different geographical distributions of the designs” [...] “but altitude was a significant predictor of the presence of wide tools ($F_{1\ ,18}$ = 21.42, p , 0.0001) and stepped tools ($F_{1,1\ 8}$ = 24.52, p , 0.0001)” (Hunt & Gray, 2003 p.871). Instead, they argue that the stepped tool – the most common tool type made across the majority of Grande Terre – represents the most advanced form, with a thin tip for inserting into small holes and a wide base providing increased rigidity and a secure hold. The wide and narrow pandanus tool forms were thought to be simpler designs from which the stepped tool evolved cumulatively (although there is no empirical evidence to support this). However, in order to determine whether this is a socially propagated culture far more data would be required to rule out asocial learning, genetic, and ecological factors.

1.3.3 *Vocal Culture*

Vocal cultures are far less contentious than primate cultural traditions; with a large body of evidence for cultural transmission of behavioural traits found in numerous bird and mammal species (Laland & Janik, 2006). While bird song was assumed to be a special case of animal culture that lacked the behavioural flexibility and scope of primate cultures, further research has shown that birds can use a variety of learning processes, for example, context-specific mimicry (Goodale & Kotagama, 2006). By analysing the spatial and temporal drift in vocal dialects, the underlying mechanisms of transmission can be investigated. Humpback whales *Megaptera novaeangliae* are a well studied case; for example, the song of whales on the east coast of Australia changed within two years to match that of the Australian west-coast population, apparently a result of the migration of just a few singing individuals from west to east (Noad et al., 2000). Bluff et al. (2010a) recently found that NC crows are able to mimic anthropogenic sounds and that the calls of wild individuals across Grande Terre exhibit regional dialects. Together, this provides good evidence for the existence of culture in NC crows based on social learning in the vocal domain, and offers a potential framework for determining how material culture might perpetuate. Congruence in the transmission patterns of vocal and material culture could suggest that NC crow tool manufacture is learnt socially through the same routes as vocal culture. For example, suppose a known stepped pandanus tool manufacturing crow moved to a population that only made straight pandanus tools. If the newcomer adopted the same straight tools and vocal dialect of the local population, or the rest of the local population adopted the newcomer's stepped tools and the accent, this would suggest the vocal and material culture were transmitted through the same horizontal social learning routes. However, ruling out genetic factors would be crucial, and this could be difficult given that recent evidence suggests that NC crows are likely to be more dependent on vertical than horizontal social transmission (Holzhaider et al., 2010b; Holzhaider et al., 2011), as I discuss next.

1.3.4 Social and Ontogenetic Influences in the Development of Tool-Use

The influence of social learning on the development of tool-use in NC crows was first studied under controlled laboratory conditions using four hand-raised juveniles. Two crows given the opportunity to interact with human tool-using demonstrators developed an interest in tools faster than those without a demonstrator, but all crows successfully learnt to use stick tools within 80 days of hatching (Kenward et al., 2006). The same juvenile crows were next presented with *Pandanus* sp. leaves, and stick tool materials were removed from their aviaries. One individual successfully tore off a section of leaf resembling a straight (non-stepped) pandanus tool on the first day of the experiment, and immediately used it to extract food, repeating the sequence several times. The three other crows tore the leaves into various shapes that did not clearly resemble wild tool designs (Kenward et al., 2005). This finding suggests that pandanus tool manufacture is at least partially inherited, and that social learning is not necessary for the manufacture of basic tool forms; nevertheless, the more complex stepped tool could still depend on cultural transmission. A subsequent experiment testing four different naïve crows' ability to manufacture and use pandanus tools found that one hand-raised individual ripped at the leaves of the supplied *Pandanus* sp. leaves indiscriminately, while the three other individuals (all caught as adults) did not touch the leaves at all (Hunt et al., 2007). The authors suggest that the heightened levels of curiosity and object-directed play found in juvenile crows in Kenward et al.'s (2005) study could facilitate the innovation of pandanus tools by trial-and-error learning. Furthermore, naïve adults' lack of interest in making pandanus tools implies there is a pandanus tool ‘learning window’ during early development similar to that of tool-use in woodpecker finches (Tebbich et al., 2001). Hunt et al. (2007) next provided the four naïve crows with ready-made pandanus tools, pre-inserted into baited holes. The hand-raised individual and a single wild-caught adult successfully used these tools to extract meat 3 times each, however, the authors claim that at least half of these extractions were due to chance ‘snagging’ events, where withdrawing the tool passively brought the meat with it. As such, the authors could not determine whether these crows were demonstrating active pandanus tool-use.

A detailed study of the ontogeny of wild pandanus tool manufacture followed the development of the behaviour in five crow family groups on the island of Maré, where the crows manufacture straight pandanus tools exclusively (Holzhaider et al., 2010a). Within two to three months of hatching, four of the six juveniles were manufacturing rudimentary pandanus tools on the baited tables. However, until six months of age they continued to use tools left behind by their parents more frequently than the tools they manufactured themselves. Juveniles also tended to make their first tools from leaves that were already damaged by their parent’s aborted attempts at tearing tools from the *Pandanus* spp. leaves. Adult-like tool manufacture techniques emerged at four to six months old and their manufacture speed gradually increased with age, but the juveniles took longer to make these tools than their parents for the duration of the study (16 months). These findings support the theory that trial-and-error learning during an early learning window plays a major role in the development of pandanus tool manufacture; but social learning in the form of stimulus enhancement and parental tolerance of juveniles were also deemed key factors. Juvenile crows continue to be tolerated by their parents, and even occasionally fed by them after they are two years old (Holzhaider et al., 2011), providing ample opportunity for vertical transmission of tool manufacture techniques through ‘epistemic niche construction’ (i.e. the tool manufacture ‘knowledge’ is dependent on parents altering a juvenile’s environment to promote continuation of the knowledge) (Laland et al., 2000). Holzhaider et al. (2010a) argued that the four sequential stages of tool-use they discovered, and the slow development of proficient tool manufacture were inconsistent with the speed demonstrated by the captive crow in the Kenward et al. study (2005). This discrepancy could highlight qualitative differences in the ontogeny of tool-use in captive and wild conditions, but it should also be noted that these studies present data from a small sample of individuals from (presumably) genetically distinct populations. Future studies of social learning in NC crows should investigate the transmission of stepped-tool designs. Cross-fostering experiments could be used to establish the hereditary versus social mechanisms in stepped tool manufacture, but these experiments would probably require aviaries on Grande Terre (for access to *Pandanus* spp. tree crowns and suitable crow populations) and a relatively large number of breeding pairs for sufficient sample sizes, aside from the ethical considerations of destructively interfering with numerous populations.

1.4 Tool-use Ecology

1.4.1 New Caledonian Crows’ Basic Ecology

Aside from their tool-using abilities, New Caledonian crows fill much the same ecological niche as other *Corvus* species around the world; acting as generalist scavengers of carrion and other birds’ eggs, and foraging for fruit, invertebrates (including larvae, and snails), seeds, and flowers (Guillemain et al., 2002; Kenward et al., 2004). Male NC crows are larger than females, but otherwise there are no obvious sexually dimorphic aspects of their morphology, and both sexes use tools (Kenward et al., 2004). Their large wing area creates low wing loading, suggesting their flight dynamics are suited to short flights within the canopy (Kenward et al., 2004), and this is supported by field observations (e.g. Rutz et al., 2007). Initial observations of social structure suggested NC crows live in small family units of a mating pair with juveniles from one or two clutches (Hunt, 2000b; Kenward et al., 2004). Holzhaider et al. (2011) provide more specific details of social structure from a study recording the interactions between marked individuals at feeding tables. This study confirms that NC crows live in small family groups, based on long-lasting pair bonds that persisted for the duration of the study (nearly four years), with one exception where an adult died. Juveniles remain close to their parents until the following breeding season, and parents were found to tolerate, and even feed their offspring of more than two years old. However no evidence was found to suggest juveniles cooperated in raising their younger siblings. Paired adult males were not found to defend absolute territories, and were tolerant of numerous non-related individuals (primarily submissively displaying juveniles, but also other submissively displaying adults). Holzhaider et al. (2011) suggest NC crow social structures are similar to the linear and stable hierarchies found in cooperatively breeding carrion crows *Corvus corone* (Chiarati et al., 2010). Our understanding of the social structures of the marked population at our Gouaro-Déva study site (see Figure 1-1) based on radio-tracking and other interactions (such as experiments, or trapping) broadly concur with Holzhaider et al. (2011) (Bluff, Troscianko & Rutz, unpublished data). However, we found that medium to large congregations of individuals (>5) could form at any time of day, and when large amounts of carrion are available (e.g. a dead deer or trapping bait) large groups (>10) could form. Nevertheless, with regards to tool-use (rather than feeding on carrion in large groups), the social structure of NC crow families suggests any socially propagated cultural traditions are far more likely to spread through vertical than horizontal transmission.

1.4.2 The Ecological Significance of Tool-Use

In order to learn more about the conditions that maintain (and perhaps, originally promoted) tool-use in NC crows we must determine its significance in their ecology qualitatively and quantitatively. For example, what types of tool-acquired food do NC crows consume, what fraction of their daily nutritional requirements depends on tool-use, and how efficient is tool-use in comparison to other foraging modes? The ecological importance of tool-use in the woodpecker finch was studied by Tebbich et al. (2002). This study revealed how individuals in the arid zone – where food availability is unpredictable and sometimes scarce – used tools to obtain half of their prey, while individuals in the humid zone used tools less frequently. Tebbich et al. (2002) argued that this unpredictability drove the evolution of tool-use in woodpecker finches, allowing them to access otherwise inaccessible prey. Wild capuchin monkeys (*Cebus libidinosus*) using stones to dig for tubers and roots may also have adopted tool-use in response to periods of limited in food availability in harsh, arid habitats (Moura & Lee, 2004). This issue is somewhat contentious (Lee & Moura, 2005; Visalberghi et al., 2005), and other lines of evidence suggest low predation risk, high levels of terrestriality and increased parental provisioning correlate better with tool-use in wild capuchins than food availability (see Ottoni & Izar, 2008). New Caledonia currently has only mild seasonal variation in weather across different habitat types, so unpredictable limitations in food availability (i.e. excluding food sources that vary seasonally) are unlikely to account for NC crows’ evolution of tool-use across all habitat types (although we know little about their possible ancestors’ situation). Interestingly, NC crows and tool-using capuchins do share parallels with regards to low predation risk (brown goshawks *Accipiter fasciatus* are the NC crows’ only known predator, and these are moderately rare on Grande Terre), high degrees of terrestriality (Rutz et al., 2007), and substantial parental provisioning (Holzhaider et al., 2011). Conducting a systematic tool-use survey in NC crows similar to that of Tebbich et al. (2002) is unfortunately exceedingly difficult. The docile nature of woodpecker finches permitted field observations of marked individuals from <10 m, allowing easy identification of behaviour and prey items. In contrast, during >800 combined hours of radio tracking NC crows at our Gouaro-Déva field site we only observed tool-use a handful of times, while other sources of evidence (such as tools left behind in larva burrows) suggested that tool-use was far more common in our marked population than radio-tracking would lead us to believe (Bluff et al., 2010b). Early studies of tool-use in wild NC crows relied on direct human observation, which in practice required provisioning of bait or prey in artificially high densities to draw in crows (Hunt, 2000b; Hunt et al., 2006). These studies could therefore only speculate as to the ecological relevance of the observed behaviours due to experimental manipulation of the difficulty of the task and/or the abundance of prey/bait. The elusive nature of wild NC crows called for novel methods to reveal their natural behaviour, leading to the development of animal-borne video cameras (Rutz et al., 2007). These miniature cameras could provide nearly an hour of footage transmitted in a single stream after an initial 24 or 48 hour delay to allow habituation. 18 camera deployments at our Gouaro-Déva study site yielded 451 minutes of footage (discussed further in section 3.1), which enabled rough estimations of tool-use frequency, foraging efficiency and generated new discoveries, including a new tool material (grass stem) and tool foraging mode (ground-sweeping). While this was an excellent proof-of-concept, the effort required in trapping, radio-tracking and capturing streamed footage limited its practicality; gathering sufficient sample sizes to estimate the overall significance of tool-use in NC crows would have been costly. Instead, we targeted the known tool-use hotspots using motion-triggered cameras together with systematic tool-removal (Bluff et al., 2010b)[1]. The camera taps provided 1797 hours of video surveillance at active Cerambycid larva sites (heavily degraded candlenut tree remains) over 111 days; during which a total of 317 site visits by 11 marked individuals from our marked population were recorded in addition to at least three additional unmarked individuals. A total of 35 larva extractions were videoed, of which the majority (71%) were immediately preceded by insertion of a tool into the same burrow. The 193 discarded tools we collected from burrows showed that wild NC crows selected longer than average sticks from the raw tool materials available in the leaf litter, and that they used longer tools for probing in deeper burrows, supporting data from laboratory studies which show captive NC crows could select tools of a suitable length and diameter for a specific task (see section 9.2.3; Chappell & Kacelnik, 2002; Chappell & Kacelnik, 2004). We also found that foraging success varied markedly between individuals; the most proficient adults could achieve larva extraction rates of 0.22 (individual identification number: HE1) and 0.19 (HC4) larvae per minute present at camera sites. In contrast, two nutritionally independent, immature NC crows probed with tools unsuccessfully for long periods at sites where proficient adults successfully extracted larvae, achieving just 0.003 larvae per minute (EK2),

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[1] Although I am co-author on Rutz et al. (2010) and Bluff et al. (2010b) these studies were primarily driven by C. Rutz and L.A. Bluff respectively, and as such I am reviewing their contribution rather than submitting them as my own work.

or failing to extract any larvae in 195 minutes at camera sites (HK2). Although this study only presented proficiency data from two immature crows there was no reason to believe that these were unusually incompetent individuals, this implies that discovering and/or extracting larvae requires a considerable degree of individual or socially acquired skill that takes over a year to develop post-fledging. Detailed studies of the ontogeny of pandanus tool-use and manufacture (discussed in section 1.3.4) also highlight the long period taken for immature NC crows to become proficient tool-users (Holzhaider et al., 2010a; Holzhaider et al., 2011).

The comparatively small number of tool-use extractions and individuals observed in studies using motion-triggered cameras (Bluff et al., 2010b) and crow-cams (Rutz et al., 2007) make quantification of the nutritional significance of tool-acquired food in the wild NC crow diet difficult. The use of stable isotopes provided an innovative means for determining the contribution of different food sources to crows' diets from the blood and feather samples of 22 crows, circumventing the difficulties of observing wild individuals and permitting suitably large sample sizes and time scales (Rutz et al., 2010). Carbon and Nitrogen occur naturally in two stable isotope forms: ^{12}C and ^{13}C, ^{14}N and ^{15}N. The relative proportion of carbon isotopes (δ^{13}C) depends on the nature of the primary producer fixing the carbon, and is carried relatively unchanged up the food chain. In contrast, the heavier stable isotope of nitrogen (^{15}N) tends to build up through the trophic levels, so that the highest predators in the food chain have the largest proportion of ^{15}N (δ^{15}N) (Michener, 2007). We collected blood and feather samples from 22 NC crows at our Gouaro-Déva field site, including 9 juveniles, 7 immature adults and 6 adults (Rutz et al., 2010). In addition we sampled all known and speculated food sources, basing our selection on confirmed observations (e.g.

those made during radio-tracking) and likely but unconfirmed food sources, such as small insects. The study rationale and a 2D plot of the $\delta^{13}C$ by $\delta^{15}N$ levels of food samples and blood and feather samples are illustrated in Figure 1-5.

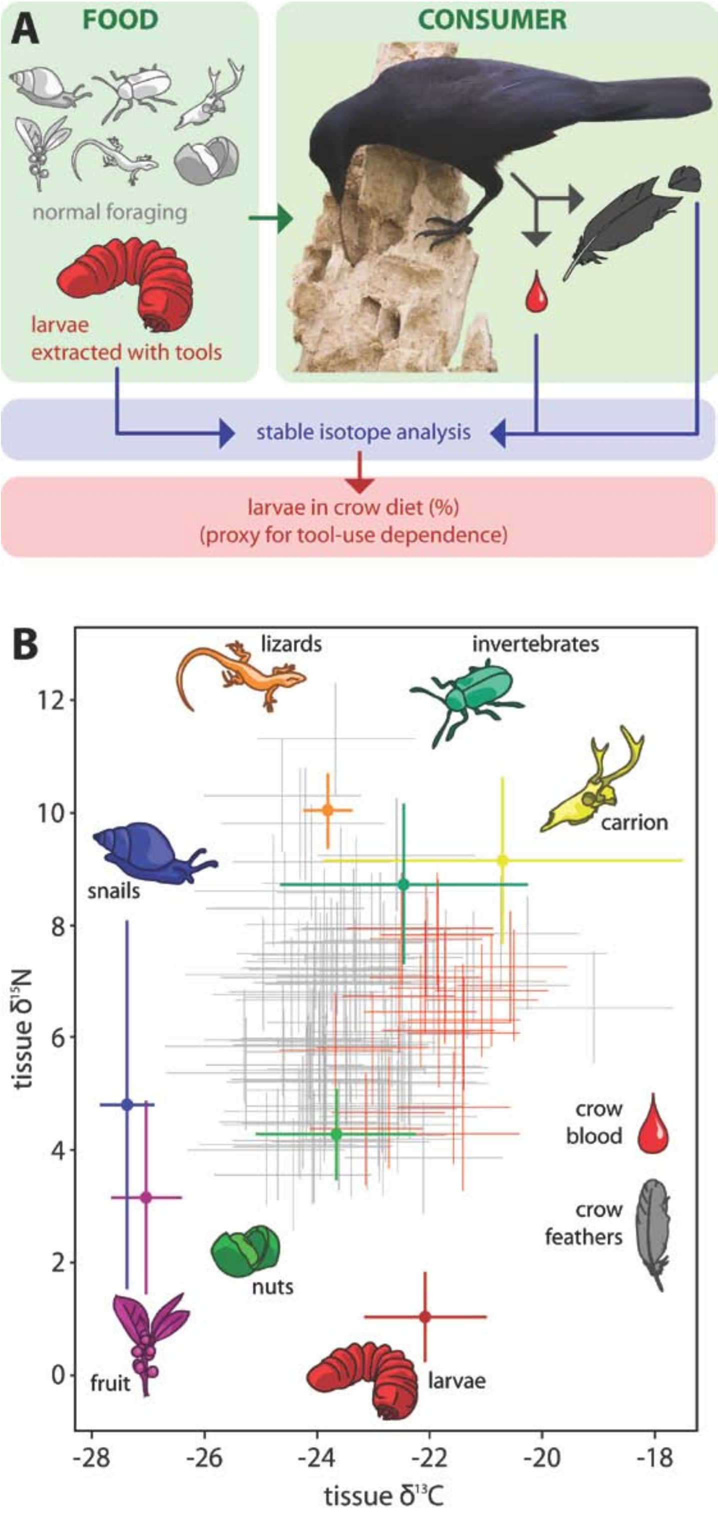

Figure 1-5. Stable isotope analysis – Fig. 1 from Rutz et al. (2010). (a) Study rationale; we sampled known and speculated NC crow food sources, and blood and feather samples from trapped individuals, then compared the $\delta^{13}C/\ \delta^{15}N$ isotope ratios observed in NC crows to those of their food sources to determine the likely contribution of each food source. (b) 2D plot of observed $\delta^{13}C/\ \delta^{15}N$ ratios in the putative food sources (mixed colours) and blood (red crosses) and feathers (grey crosses); error bars show the degree of uncertainty based on trophic enrichment factors.

Bayesian isotopic mixing models (Parnell et al., 2010) were used to calculate the likely contribution of each food source to each crows' diet. Essentially, this model adds and subtracts the seven food sources, and varies their proportions to find the most likely contribution of each for observed isotope ratios found in the crows' blood and feathers. The technique also allowed us to observe two temporal scales; blood samples reflected the crows' food consumption over the few days prior to capture, while metabolically inert feathers can indicate what the crows were eating a few weeks or months earlier depending on the feathers' moult cycle. Cerambycid larvae were found to have a distinct $\delta^{15}N$ signature (see Figure 1-5B), which was significantly lower than all other food sources; presumably due to the nitrogen-fixing symbionts in their guts. Initial model estimates suggested that 45.4 ±9.8% (feathers) or 46.1 ±8.3% (blood) of the NC crows' overall lipid intake came from these larvae, while candlenuts made up the second most important source. Both of these food sources rely on tool-use to some degree; Bluff et al. (2010b) showed that the majority of larvae were extracted following tool-use, and nut-dropping in NC crows is arguably more advanced than that used in other examples of nut-dropping (Hunt et al., 2002).

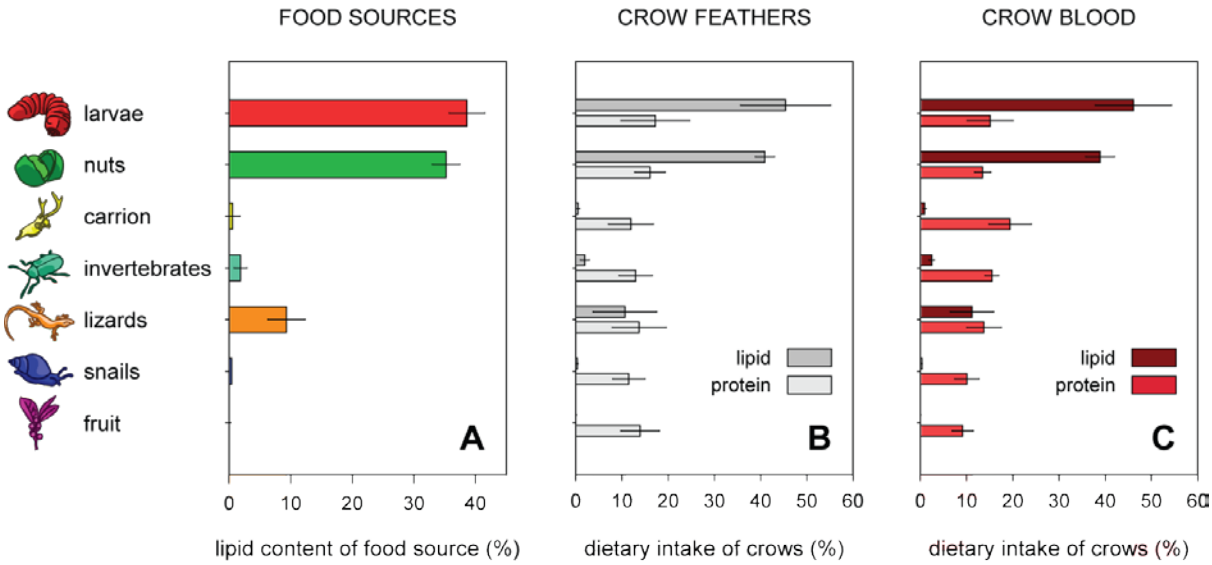

Figure 1-6. Data from food sampling and stable isotope analysis – Fig. 2 from Rutz et al. (2010). (a) Lipid content of the seven putative food sources, showing that larvae and nuts are energy-rich foods, and predicted dietary contributions of lipid and protein based on feather samples (b) and blood samples (c). The data show that larvae and nuts (both from candlenut trees) contribute to the majority of the NC crows' dietary lipid intake, while contributing a similar amount of protein as other food sources.

Energy calculations demonstrated that just 2.98 ±0.28 larvae of mixed body size would be sufficient to satisfy an NC crows' daily energy requirement, highlighting the considerable energetic rewards for efficient tool-users. Rutz et al. (2010) go as far as to suggest that the recent introduction of the candlenut tree by humans could have provided opportunities that led to the rapid evolution of tool-use in NC crows, although, as I discuss in section 1.2, it would seem unlikely that this could account for the population-wide use of tools across different habitat types, or for manufacture of pandanus tools or hook tools in quite different foraging contexts. However, an unfortunate error was made in the estimations of Cerambycid larva energy content by Rutz et al. (2010); dry-mass values were not converted back to wet-mass values, resulting in an overestimation of their energetic value (Rutz et al. in press). Revised estimates found that NC crows were consuming 3-4 larvae per day; while this rate is within the upper estimates observed in proficient crows by Bluff et al. (2010b), we consider this higher than expected for the average individual. There are a number of potential explanations for this discrepancy; such as an underestimation of intake rates or temporal differences in intake rates between isotope sample collection and video-based estimates, or the energy-budget models may have overestimated the intake rates. But perhaps the most likely scenario is a missing food source; any missing food source must also share the same low $\delta^{15}N$ levels of Cerambycid larvae, suggesting they too are likely to be xylophagous (wood-boring) insects, which are in turn also likely to be extracted using tools. Further observational studies are required to identify this missing food source, which NC crows must acquire outside of the well-studied candlenut tree foraging opportunities. The apparent fact that we may have missed an important tool-acquired food source in our heavily observed NC crow study population is testimony to their elusive nature.

1.4.3 Summary

After years of observations and fieldwork in New Caledonia there are still many unanswered questions relating to tool-use in wild NC crows. We still know very little about the development and transmission of stepped tools made in the high altitude forests; indeed we know almost nothing about these crows' basic ecology. Observing NC crows is extremely difficult in anything but fairly open terrain and this has limited us to indirect sources of data, such as pandanus tool counterpart comparisons (e.g. Hunt et al., 2001; Hunt & Gray, 2003), or stable isotope analysis (Rutz et al., 2010). But these methodologies have inherent problems, for example, counterparts are left by an unknown sample size of tool-makers with no information on specific individual's behaviour and interactions with others. Isotope analysis also depends on suitable sampling of the NC crows' food sources, which therefore depends on substantial prior knowledge of the crows' feeding habits. Crow-borne cameras have proven their utility in making unobtrusive observations of wild individuals' foraging habits and tool-use behaviour (Rutz et al., 2007), and with greater footage recovery rates and the possibility of using the system in humid forests this method could be incredibly useful in conjunction with stable isotope data to build up a more complete picture of the ecological significance of tool-use in NC crows. I present my contribution the development of a new crow-borne camera devised for this aim in Chapter 3.

Further questions have been raised by studies showing that tool-use proficiency can take a number of years to develop in wild NC crows (Bluff et al., 2010b; Holzhaider et al., 2010a). Developmental research has demonstrated the importance of social learning and an inherited motivation for tool manufacture (Kenward et al., 2005; Kenward et al., 2006; Holzhaider et al., 2010a), but these mechanisms cannot easily explain why there is such a lengthy period of high investment in tool-use learning. I address this question in Chapter 4 by investigating the difficulties posed by an apparently simple probing task in wild individuals.

2 CHAPTER TWO – GRASS-STEM TOOLS: THE VALUE OF CHANCE OBSERVATIONS

2.1 Introduction

This observation was published in Troscianko, J., Bluff, L. A. & Rutz, C. (2008). Grass-stem tool-use in New Caledonian Crows Corvus moneduloides. — Ardea 96, 283-285.

New Caledonian crows are both wary of and interested in humans, making candid observations of their tool-use behaviour frustratingly rare. Nevertheless, chance observations can provide valuable insights for testing assumptions and hypotheses, and the following observation is a timely testimony to this. Using animal-borne video cameras, Rutz et al. (2007) recently documented a novel tool material in NC crows – dry, grass-like stems, which they used for probing in loose substrate on the ground. Two tools, manufactured and used by two different adult males (ID-codes ‘CC1’ and ‘EK1’; see scene 2 of movie S2, and scenes 2 and 3 of movie S3 in Rutz et al. (2007)), were recognizably different from any previously reported tool types. Video analysis suggested that these tools were dry grass stems, but as the footage was recorded using remote wireless transmission it was not possible to recover the tools or examine the raw materials. Critics argued (Hunt & Gray, unpublished commentary) that the footage was of insufficient quality to verify the claims of a novel tool material without further documentation. My independent observation of a wild NC crow (identification code: HC3) manufacturing two tools from dry grass stems (tools A and B in Figure 2-1), and using them to forage for lizards hidden within the crevices of a fencepost verifies Rutz et al.’s claims of a novel tool material.

2.2 Methods & Results

I made the observation together with Dr. Lucas Bluff (who observed through binoculars) on 6 November 2007, under unusually favourable conditions, approximately 50 m from our field base in Gouaro-Déva, New Caledonia (21.60°S, 165.40°E). I observed the crow (ID-code ‘HC3’) for just over 2 minutes from a distance of *c*.20m, taking 45 photographs using my Canon 5D DSLR with a 100-400mm ‘L’ stabilised lens. Key events are shown in Figure 2-1, and the following timeline refers to panel sections (A to H in Figure 2-1):

12:15:48 – First photo of crow taken on the fencepost (not shown). The bird has no tool in its beak.

12:15:53 – HC3 moves to another part of the fence. The bird still has no tool.

12:16:09 – HC3 moves to the top of one fencepost with a grass-stem tool (tool a) and proceeds to probe with this tool for c. 5 seconds (A to C) before placing it on the surface of the post from where it falls to the ground (tool a could not be recovered as it had fallen amongst other pieces of dry grass). HC3 appears to look down into the crevice.

12:16:23 – HC3 has moved *c*. 30 cm from the fencepost to an adjacent horizontal fence section (D), where it is within reach of a large bundle of dry grass stems.

12:16:31 – HC3 manufactures tool B by breaking off a long section of a dry grass stem and shortening it (the missing section can be identified by comparing (D) and (E)).

12:16:33 – HC3 returns to the top of the fencepost and resumes probing into the crevice with tool b (E).

12:16:39 – HC3 looks down into the crevice, with tool b still inserted; it then resumes probing with tool b (F).

12:16:43 – HC3 leaves tool b in the crevice and picks up the first lizard with its bill (G), holding it in the bill for c. 30 seconds before swallowing it head-first.

12:17:28 – HC3 resumes probing into the crevice with tool b.

12:17:45 – HC3 catches a second lizard, and draws the lizard and tool b together out of the crevice (H). It is not clear whether the lizards were biting onto the end of the tool, whether they were wrapped around it, or whether they flushed the lizards from their hiding places.

12:17:54 – HC3 places tool B (which is now shorter and without node; see Figure 2-2) and the second lizard on the surface of the post and disentangles them by using its left foot to secure the tool and its beak to restrain the lizard.

12:17:58 – HC3 swallows the second lizard head-first and flies off, leaving tool b on the post (tool later recovered; see Figure 2-2).

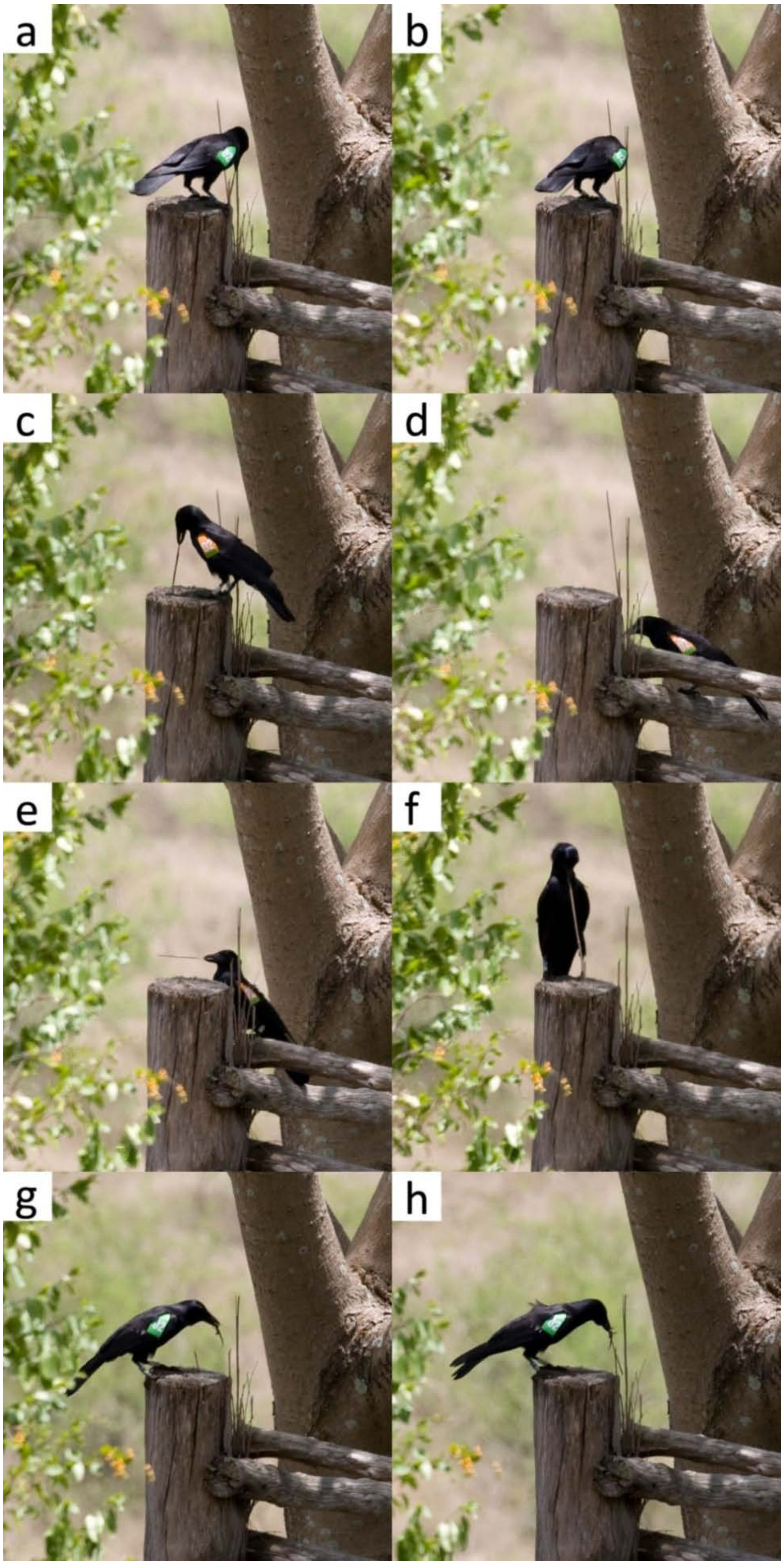

Figure 2-1. A series of photographs of a tagged NC crow using and manufacturing grass stem tools and extracting two lizards from a wooden fencepost. See main text for a timeline and description of the events.

Figure 2-2. Photograph of the recovered grass stem tool 'B' shortly after an NC crow manufactured it and used it to extract lizards from a fencepost.

2.3 Discussion

Such sustained, close-up observation of tool-use by wild crows is rare, without the use of either a hide at a baited site, or remote telemetry (see Rutz et al., 2007). The bird, an adult male, had been trapped on 15 December 2006, when it was marked with wing-tags, rings and a tail-mounted video-tag; the latter was shed prior to the present observation. Both tools used by this bird exhibited nodal segmentation (for tool A, see Figure 2-1C; for tool B, see Figure 2-1F), that was also used to identify the material as grass stem in Rutz et al. (2007). The recovery of tool B (Figure 2-2) and examination of the raw material in situ allowed me to identify the tool material unambiguously as dry grass stems, confirming the earlier observation with animal-borne cameras (Rutz et al., 2007). I should point out, however, that both tools used on this occasion were stiffer than those recorded during video-tracking, which had been manufactured by birds on the ground. My observation was made within the study area of the earlier video-tracking work (Rutz et al., 2007), so I cannot comment on the geographical extent of this type of tool-use. Tool-use in New Caledonian Crows appears to vary regionally across the island (Hunt & Gray, 2003), and it has been suggested that aspects of this species' tool technology are under the influence of cultural transmission (see section 1.3.2). Documenting regional variation in behaviours can provide important information on material cultures in non-human species (Whiten et al., 1999), and my report adds to the growing catalogue of tool materials and techniques employed by New Caledonian Crows (Hunt & Gray, 2006). A quantitative 'ethnographic' survey of this species' tool-oriented behaviour cannot rely on rare chance observations, such as the one described here. Considering the difficulty of observing the natural foraging of wild crows, animal-borne cameras are an ideal tool for discovering novel aspects of their behaviour. But this observation highlights the pitfalls of a dependency on animal-borne cameras. Future generations of cameras should provide higher quality images for analysis, and longer temporal coverage that does not rely on wireless transmission and reception of video footage (Bluff & Rutz, 2008; Rutz & Bluff, 2008).

3 CHAPTER THREE – CROW-BORNE VIDEO CAMERAS

3.1 Introduction

Animal-borne cameras can capture aspects of behaviour or ecology that are otherwise difficult or impossible to observe first hand. This field was pioneered by marine biologists, who have been able to attach cameras to a wide range of marine mammals for a number of years (e.g. Marshall, 1998). Until recently however, these cameras were far too heavy for deployment on most terrestrial mammals, let alone birds. The miniaturisation of electronics first allowed experimental cameramen to attach cameras to captive birds for wildlife documentaries. For example, the BBC's 'Animal Camera' documentary (aired in 2004) shows footage of eagles, hawks, falcons and pigeons in flight. These captive animals had been trained to wear a harness to which camera units could be attached for brief periods. The first systematic deployment of cameras on wild birds was reported by Rutz et al. (2007), who successfully attached cameras to 22 NC crows following pilot testing on captive crows. The 'crow-cam' units used by Rutz et al. transmitted footage wirelessly after a pre-defined habituation period (24 or 48 hours following release, see Figure 3-1). Crows were located using an on-board VHF transmitter, and cameramen (of which I was one) recorded the transmitted video footage through receiver units. The direct line-of-sight range of these units was approximately 300-500m using large parabolic ('satellite') dishes and helical antennae, but in practice this was dramatically reduced by any vegetation because the high frequency carrier wave used (2.4GHz) refracts only around very small objects (in comparison to VHF at *c*. 150MHz), and it is absorbed by the water in foliage (Bluff & Rutz, 2008). This meant there was always a trade-off between higher quality footage (with fewer 'white-outs' due to loss of reception), and getting too close to the target animal and flushing it away or disturbing its previous behaviour. The relatively open farmland, savannah and dry-forest terrain study area of these crow-cam deployments was moderately well suited to the methodology. Nevertheless, even with two receiver cameramen 66% of all transmitted footage was not recovered due to failure to capture the footage as it was broadcast. These limitations render the methodology impractical in humid forest terrain, where keeping up with crows flying through the canopy while carrying large parabolic dishes would be extremely difficult, if not impossible with a reduced operating range. Observations of NC crows in the humid forests are exceedingly rare in comparison to dry forest habitats for a number of reasons: (i) the abundance of NC crows appears to be lower in humid forests, (ii) the crows appear to be more wary of humans in the humid forest (possibly because there is less large game hunting to attract crows after gutting game on site or failing to recover terminally injured or killed game), (iii) the crows rarely approach the ground, flying through the over-storey or above the canopy, and (iv) dense foliage limits visual observations to just a few metres (pers. obs.). Yet some of the most interesting observations are likely to be made in the humid forest, where the crows manufacture pandanus tools (Hunt & Gray, 2003). In order to discover more about the behaviour and ecology of humid forest crows I assisted in the development of a new generation of crow-cam units which record video to onboard solid-state memory. Specifically, I contributed to circuitry testing, I built and packaged the units, I programmed the units (although source code and timer chips were supplied by Ron Joyce). I conducted fieldwork together with C. Rutz, testing prototypes on captive NC crows, trapping and tagged all the wild NC crows in this preliminary deployment, and recovering the shed units.

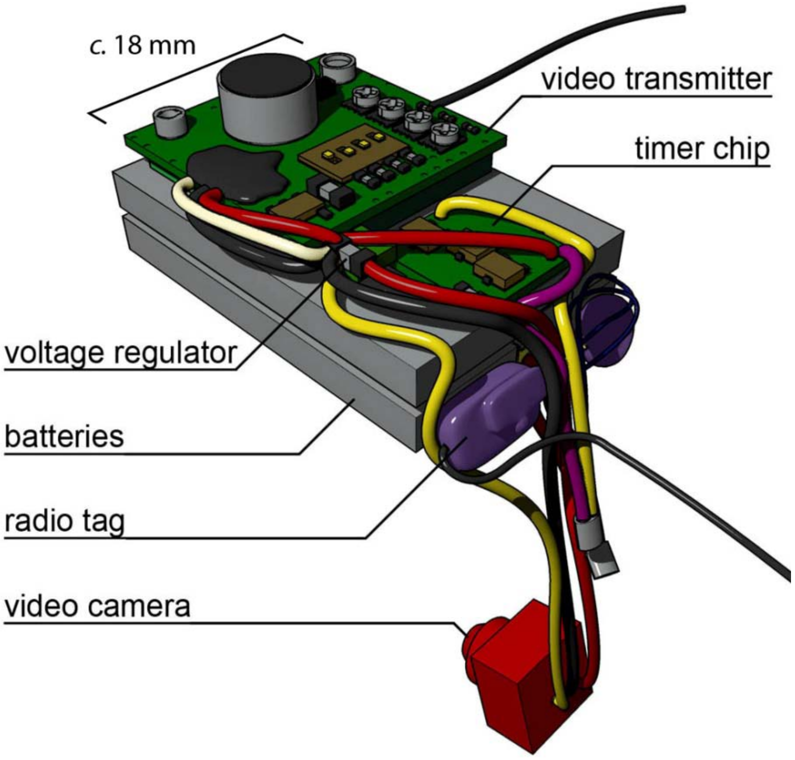

Figure 3-1. A 3D schematic of the crow-cam units used by Rutz et al. (2007), showing all of the major components. The VHF radio tag runs from an isolated silver-oxide cell and can transmit for approximately 3 weeks. All other onboard circuitry runs on the lithium polymer cells, which are sufficient for transmitting up to 70 minutes of footage to receiver cameramen on standby within <500m range.

3.2 Methods

The new generation of cameras were based on ‘mini DV’ cameras sold to consumers as miniature sports cameras or spy cameras. The units we chose could record 640x480 resolution footage at 20 frames/second to a 4 gigabyte microSD card. I sourced lithium polymer batteries with different capacities (and weights), from a stated capacity of 160mAh to 300mAh. The largest batteries suitable for deployment yielded approximately 100 minutes of footage, and the smallest approximately 60 minutes. The cameras were controlled by a timer board developed by Ron Joyce. These were small circuit boards weighing approximately 0.49g that could control power to the camera unit through a transistor, and start/stop recording by simulating a button depression using a second output; all controlled by a programmable PIC microchip. The microchip could be reprogrammed with code specifying almost any desired filming schedule, specifically, the number of hours to delay before the first shoot, the length of first shoot in minutes, and length of the subsequent delay in minutes, and so on. Acquiring the recorded video data depends on recovering the units through one of two methods: (i) re-trapping the crow, or (ii) locating units after they have been shed. A VHF transmitter on the crow-cams allowed us to locate shed units within a range of approximately 500m; although this was highly dependent on the terrain in which the unit fell. VHF transmitters were powered by a single silver-oxide cell, and depending on the battery size (and weight) the VHF tags could continue transmitting for up to 5 or 9 weeks, providing a practical time window for the tags to shed. Two measures ensured crow-cams were shed quickly and reliably after deployment: (i) I attached the cameras to central tail feathers using thin sections of rubber balloons that degrade in ultraviolet light and through wear and tear, (ii) I deployed cameras prior to, or during the moulting season (January to February, (Rutz et al., 2007)) as an extra failsafe to ensure that cameras were shed within a few weeks of deployment (see Figure 3-2).

The solid-state video camera circuitry was approximately 1-2g heavier than the wireless broadcasting board in the previous generation of crow-cams. Therefore, I set out to reduce overall unit weight by creating a lightweight packaging system. The first generation crow-cams were packaged in heat-shrink tubing, which accounted for 3-4g of unit weight. I developed a process for creating thin (0.1-0.15mm) sheets of thermoplastic (polycaprolactone, sold under the brand name 'Polymorph' in the UK) that could be moulded onto the units and removed with ease (e.g. the sheets did not exhibit 'memory' typical of thin plastic sheets, and were highly cohesive). This material could package units with only 0.6-0.7g of material, a substantial weight saving which offset the slightly heavier circuit board.

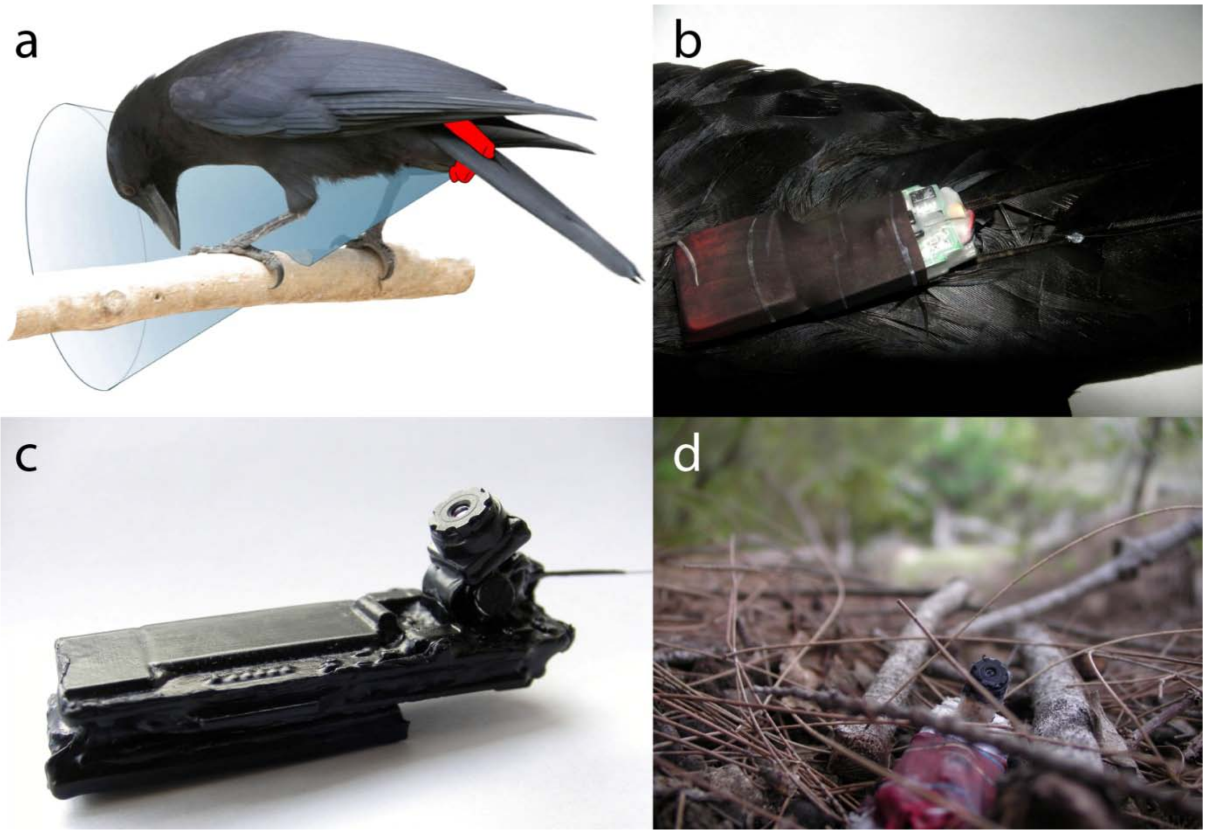

Figure 3-2. (a) Schematic showing the mounting position of crow-cam units. (b) A second-generation crow-cam unit attached to the two central tail feathers of an NC crow, held in place with a section of rubber balloon that degrades when exposed to ultraviolet radiation in sunlight. (c) Photograph of a fully assembled crow-cam unit, packaged in thin 'Polymorph' sheets. These cameras weigh 12-13 g, and are 54mm in length (excluding the VHF antenna). (d) A shed crow-cam on the forest-floor awaiting recovery.

3.3 Pilot Deployment

I deployed 19 second-generation crow-cam units from 12 December 2009 to 18 January 2010 in our dry-forest study site. I trapped crows using a whoosh-net established at coordinates -21.5566 S, 165.3158 E, with butchers' offal as bait (this included bones, lungs, liver, skin & fat from cows and pigs). Crows were trapped in the evening (1600-1800) and transported back to our base-camp where subjects' weight was immediately recorded, and blood samples were taken for isotope analysis, DNA analysis, and sexing. We took blood samples from all subjects by piercing the vena ulnaris with a syringe needle and collecting drops of blood with sterile capillary tubes (see Rutz et al., 2010 supplementary online materials, all relevant permits were acquired by C. Rutz). I then released the crows into an aviary overnight (dimensions: 3x3x2m, with perches, water, cat food supplied *ad libitum* (dried food, rehydrated with water) and pieces of beef heart). Based on each crow's weight I assembled suitable crow-cam units overnight, aiming to deploy a unit no greater than 5% of body mass on each individual (see section 3.3.3 for a discussion of weight justification). Crows were processed in the morning (gap colouration photographs for ageing, taking morphometric measurements, feather samples, adding leg bands and coloured wing-tags for field identification, and securing crow-cam units) (see Rutz et al., 2010 supplementary online materials), and were released as soon as possible. The maximum period any subjects were held in captivity was 18 hours, and all subjects ate the supplied food. All bait was removed from the trap-site so that it did not interfere with crow-cam shoots.

3.3.1 Recovery & Modifications

I deployed a total of 19 cameras on wild crows, recovering 11 units; see Table 1 for summary data and Figure 3-3 for still-frame samples of footage. All recoveries were located through VHF telemetry rather than re-trapping. Early unit recoveries highlighted attachment and design weaknesses that I was able to address in later models. VHF signals were identified as failing or absent in a small number of deployments, and some recovered units showed substantial damage to the aerial and VHF battery connection. As a result I moved the VHF tags to a less exposed position within the crow-cam units and ran the first 50mm of aerial along the body of the units for protection. A second design weakness was the camera itself; in crow-cam deployment 11 (‘cc11’ hereafter), the crow managed to tear through the ribbon linking the camera to the rest of the unit before filming started, resulting in a total loss of footage. In subsequent designs I reinforced the camera’s ribbon connection to the circuit board with carbon fibre. I also rectified a potential attachment weakness; tail-feather barbs obstructed the camera lens of cc5, resulting in 53% of footage being of insufficient quality for analysis, as opposed to an average of 4.2% across all other deployments. Therefore greater care was taken to trim the tail-feather barbs around the camera lens in subsequent deployments. Following these modifications the unit recovery rate increased to 80% with no loss of footage or significant feather obstruction (4 out of 5 deployments recovered, with the 5th unit still attached to cc16 at the end of the field season, presumed to have detached shortly thereafter).

3.3.2 Video Scoring

I scored footage to a resolution of 1 second, viewing footage in Media Player Classic software (version 6.4.9.1), and using a macro script (autohotkey version 1.1.0) to import the time of events as they start and stop into Microsoft Excel (version 12.0.4518.1014). Each crow's overall activity, location and bill interactions were categorised, together with additional notes and the duration of all flights lasting >15 frames (0.75 seconds). Categories are shown in Figure 3-4 together with respective overall duration times for each individual and average percentages. Prey encounter rates were determined by counting the number of discrete food items captured on video footage, then dividing this by the total analysable recording time for that individual. The type of food item was recorded as precisely as possible. The percentages of time devoted to an identified behaviour were calculated in Excel, but standard error values are not given because the count data are not normally distributed.

3.3.3 *Ethical considerations*

Previous studies on the impact of long-term radio-tag deployments suggest that tags should be <3-5% of animal body mass, with smaller percentages recommended for birds and aquatic animals (Kenward, 2001; Withey et al., 2001; Demers et al., 2003; Moil et al., 2007). However, our tags were only likely to remain attached for short periods of a few days, or, in the unlikely event that the rubber attachment degrades slowly, until the feathers moult (a few weeks at most). Rutz et al. (2007) discuss the ethical implications of the weight of crow-cam deployments of up to 5% of body mass, noting that the foraging behaviour and flight behaviour of the tagged crows was not noticeably altered. New Caledonian crows very rarely fly more than *c*. 100m, instead choosing to fly from tree to tree (pers.obs. of wild un-marked individuals and following radio-tagged individuals as they travel amongst or alongside unmarked individuals), and as such, the additional energy costs incurred to their usual foraging behaviour are likely to be much lower than other birds which stay on the wing for long periods (e.g. sea birds). Rutz et al. (2007) note that crow survival was not apparently affected by crow-cam attachment based on a number of resightings of tagged crows. Since publication we have made even more resightings of previously tagged individuals, suggesting the long-term effects of crow-cam tagging are minimal. Nevertheless, trapping, handling and marking wild animals always presents dangers to the individuals and will inevitably cause a degree of discomfort or suffering; it is therefore imperative that the value of the research is weighed against these considerations and alternative means for collecting the data are pursued wherever possible. A number of factors make NC crows good candidates for tagging: (i) they are elusive and extremely difficult to observe in a natural context (i.e. away from feeding tables or baited sites observed from hides or motion-triggered cameras at activity hotspots (Hunt & Gray, 2004b; Bluff et al., 2010b)); (ii) they are abundant and comparatively easy to trap at our dry-forest field site; (iii) we are in a good position to continuously monitor the impact of camera deployments in our marked population; (iv) evidence from previous deployments suggests the natural behaviour and ecology of NC crows are not adversely affected (Rutz et al., 2007); (v) we know comparatively little about the basic ecology of this species, which is one of the most sophisticated tool-users in the animal kingdom (Hunt, 1996; Weir et al., 2002), and as such they present one of the most interesting models for investigating the evolution of tool-use in a non-human.

3.4 Results

Crow-cam unit weights were ≤5% of the crow's body mass in all deployments, with a pooled average of 4.3% of body mass overall (see Table 1). Average unit weight with higher-capacity batteries was 13.1g, and 12.6g for the smaller-capacity batteries, with the lightest unit weighing just 12.32g (for reference, a £2 coin weighs 12.0g). Recovered crow-cams fitted with the larger battery yielded an average of 92.5 (n=4) minutes of footage per deployment, while the smaller battery averaged 71.2 (n=6) minutes of footage. The shortest filming duration was 60.0 minutes, and the longest was 98.2 minutes.

I recovered a total of 777 minutes of footage from 10 units, however, one unit (cc9) detached after 31 minutes of recording, leaving a total of 712 minutes of footage from crow-borne cameras. Of this, 637 minutes (89%) was of sufficient quality for basic analysis of the crows' location and/or activity, although the percentage of analysable footage rises to 96% if cc5 is excluded.

Figure 3-3. Still frames from crow-cam footage. (a) An example of eating an identifiable fruit (arrowed, a type of mahogany tree known locally as acajou *Semecarpus atra*). (b) Feeding an insect to a chick on the nest. (c) Manufacturing a hook tool. (d) Probing with a hook tool in a paperbark tree.

Deployment number	Crow ID	Crow weight (g)	Crow-cam weight (g)	% body mass	Notes
1	CC5	295	13.38	4.54	Recovered
2	AK7	255	12.63	4.95	Recovered
3	EK4	250	12.50	5.00	Lost (confirmed faulty VHF)
4	HE8	360	13.29	3.69	Lost
5	AC6	315	13.09	4.16	Recovered (feather obstruction)
6	HE5	350	13.39	3.83	Lost (confirmed faulty VHF)
7	HC2	290	12.32	4.25	Lost
8	HE4	310	12.82	4.14	Lost
9	EC5	310	12.88	4.15	Recovered (detached early)
10	HE6	315	12.98	4.12	Lost
11	HC1	310	12.93	4.17	Recovered (camera damaged)
12	HE7	330	13.07	3.96	Recovered (damaged, partial loss)
13	HC1	305	13.62	4.47	Lost (suspected VHF fault)
14	EC3	255	12.51	4.91	Recovered
15	HE2	340	13.09	3.85	Recovered
16	RB73	265	12.56	4.74	Lost (attached at end of season)
17	CK1	345	13.13	3.81	Recovered
18	AC5	250	12.48	4.99	Recovered
19	EC7	280	12.55	4.48	Recovered

Table 1. Details of crow-cam deployments.

3.4.1 Video scoring

Crows spent the majority of their time in trees (78%), with all crows spending a significant proportion of their time in paperbark trees (*Melaleuca* spp.), which averaged 41% of all analysable footage. On average crows were observed on the ground for 8.8% of the time, although there was substantial individual variation: cc9 and cc14 were not observed on the ground and cc19 spent 23 minutes on the ground (31% of footage). All crows were observed flying, which made up 1.7% of combined footage. Flights were on average 4.02 seconds in duration, the longest being 24 seconds. See Figure 3-4A for a breakdown of time spent in each location by each individual.

The crows' behaviour could be inferred in 77% of footage, although the distinction between walking/hopping, foraging, and feeding is dependent on observations of the bill, which was observed in activities totalling 31% of the total analysable footage. See Figure 3-4B for each crows' activity data.

Observing bill activities and interactions suggests crows dedicate on average 44% of their time to probing through the bark and crevices in paperbark trees. This form of foraging was characterised as moving from branch-to-branch, looking into crevices and tearing off sections of the soft, flaky bark. Four novel prey types were identified during paperbark foraging. These are: ants nesting within deadwood, unidentified wood boring insect larvae *c*. 1-2 cm long, unidentified small bright green insect larvae *c*. 0.5-1 cm long (which I have previously observed beneath paperbark bark), and large adult insects (probably crickets and cicadas). Crows also spent a considerable amount of time foraging for, feeding on, or carrying other common classes of prey, including insects, carrion, fruit and nuts from candlenut trees. Another novel food source was a frog; cc5 was observed feeding on a frog and then tearing off portions and giving them to a begging juvenile unmarked crow (identified as a juvenile from its pink gape).

Four crows were observed using tools in eight separate instances and two crows were observed manufacturing hook tools (see Figure 3-3C & D). Tool-use, defined as tool-probing, bill-probing following tool-probing in the same hole/crevice, and carrying tools accounted for 6.9% of all observed bill activities and tool manufacture accounted for 1.9%. A number of instances were recorded where the crows' location and body movements were consistent with tool-probing without verification of this behaviour from bill observations. If these instances are ignored, then tool-oriented behaviour is conservatively calculated at 3.7% of all recorded footage. The majority (96%) of tool-use captured on video was in paperbark trees, accounting for 1279 seconds in six instances by cc15, cc17 and cc18. All five prey items or suspected prey items acquired through tool-use were observed during paperbark foraging. The identifiable prey items were medium-sized insect larvae and large adult cricket-like insects hidden beneath the bark. One instance of tool-probing on the ground was recorded for a total of 53 seconds. During this observation cc18 probed through leaf litter and under a fallen branch using a hook-tool, which the crow had manufactured earlier. The only observation of tool-probing in candlenut deadwood was a brief 6 second observation from cc5. Unfortunately the crow's feathers obscured the footage before and after this observation, however, this visual impairment did not obstruct observations of locomotion, and cc5 remained at this position for at least 136 seconds, suggesting this tool-use bout lasted longer than the recorded 6 seconds. Two instances of hook-tool manufacture were recorded; cc15 spent 179 seconds crafting a tool from a living paperbark twig. First, cc15 snapped off a twig just above and below a branching node, it then stripped the bark and leaves from the longer, thinner branch, and worked on the node to create a hook. Cc15 continued to probe into paperbark with the hook tool for the remainder of the programmed recording session (79 seconds). The second instance of hook-tool manufacture was recorded from cc18, which made a hook tool from an unidentified tree species that was not paperbark. Construction took 59 seconds from snapping off the branch, removing leaves and bark, and fashioning the hooked end. Cc18 continued to probe with this tool for 690 seconds, including an instance where it dropped the tool onto the ground and promptly recovered it. Location, activity and bill interactions are presented in Figure 3-4.

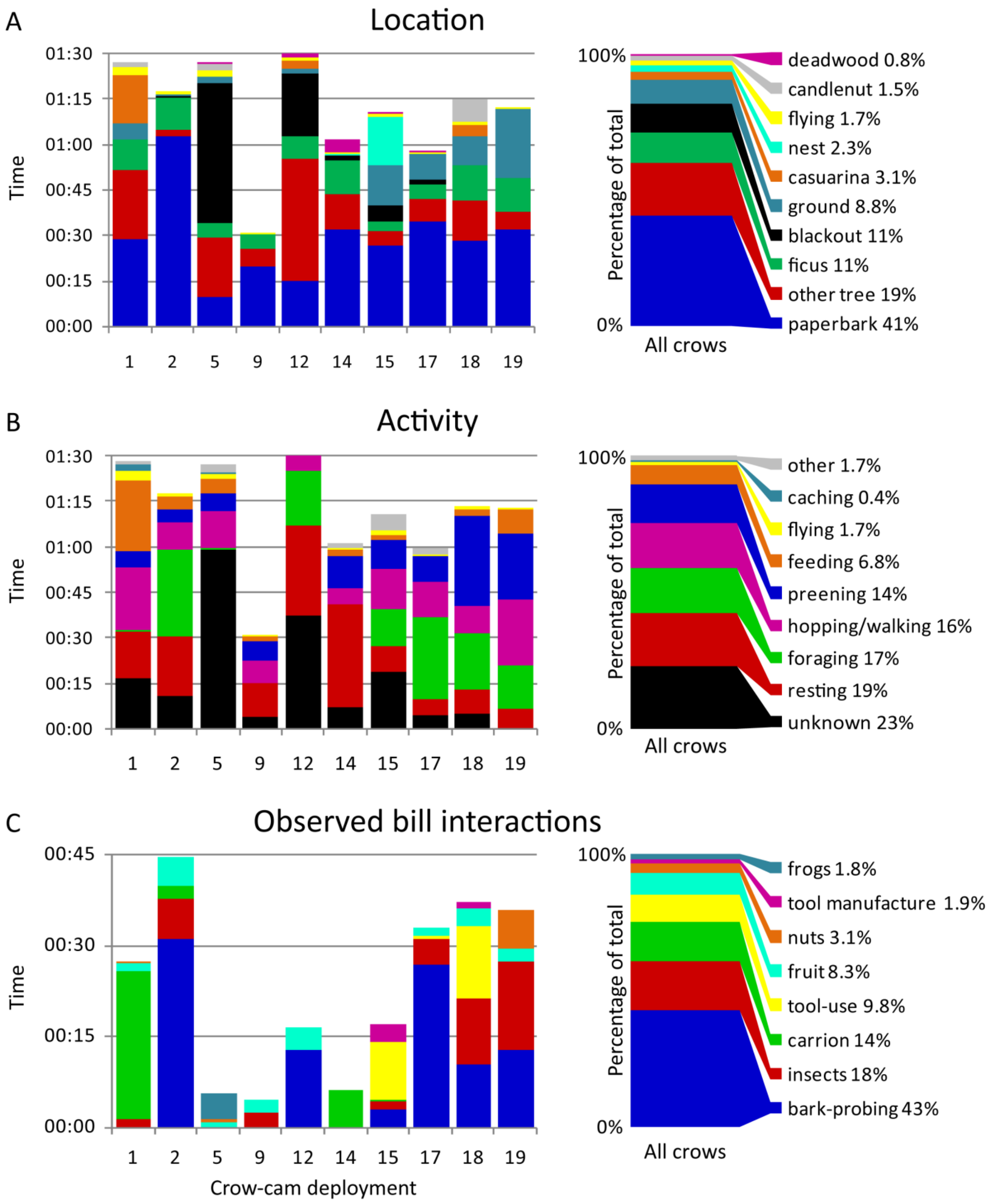

Figure 3-4. Bar graphs on the left showing the length of time each crow spent in a given location (a), different activities (b), and observed bill interactions with objects (c). Percentages averaged across all individuals for respective observations are shown on the right. *Casuarina equisetifolia* trees are common at our dry forest site on the exposed hillsides.

Food and prey encounter rates average 5.2 (S.D: 3.1) items per hour. The highest rate of 10.7 items per hour was observed in cc19. This crow encountered 9 large insects that looked like cicadas while foraging on the ground and bark-probing in paperbark trees. The lowest food encounter rate of 1.3 items per hour was observed in cc12, which was only observed feeding on fruit. For an analysis of food encounters see Figure 3-5.

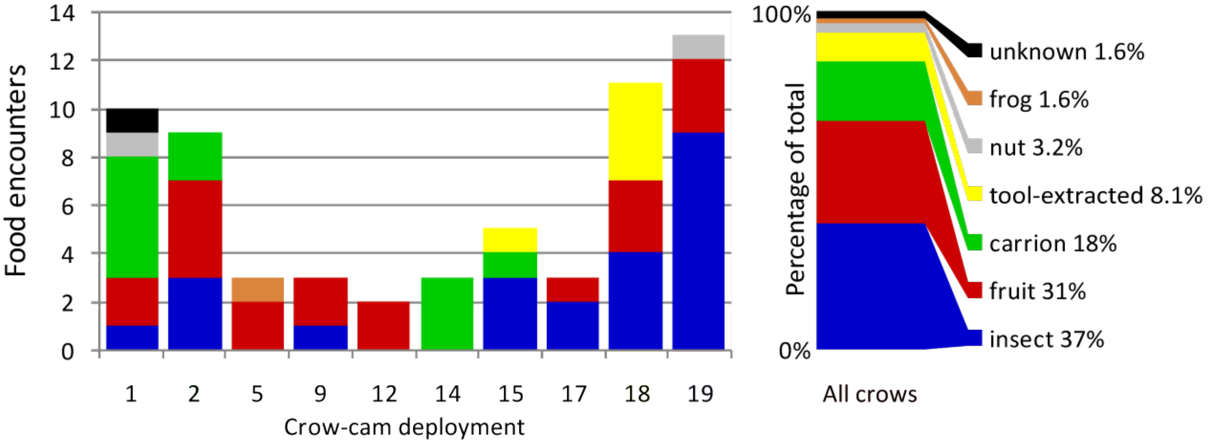

Figure 3-5. Observed food/prey encounters in each crow (left) with total proportion (right). Tool-extracted prey are invariably insects or other invertebrates, but the category 'insect' (above) refers to insects that were predated without assistance from tools.

Crow-cam footage caught unmarked crows on video a total of 21 times (counting a clutch of chicks as a single unmarked crow), and marked crows – identifiable from coloured wing-tags and ring codes – were captured a total of 7 times. In one instance cc5 captured an unmarked crow holding a tool. Other instances revealed social interactions, for example, cc14 repeatedly captured footage of the marked crow HE5. HE5 appeared to be interacting with (possibly building) a vacant nest that cc14 inspected shortly afterwards. HE5 also appeared to be provisioning cc14 with food while cc14 appeared to spend less time foraging, and more time resting than other birds (Figure 3-4B). Further evidence suggesting that HE5 was courting cc14 was provided by footage showing the two preening beside one another (possibly allo-preening given their proximity and movements, although their bills were out of shot). Cc15 was twice captured feeding newly hatched chicks on the nest with cicada-like insects that had been collected on the ground.

3.5 Discussion

Pilot deployments of new generation crow-cam units establish their field worthiness and future potential for deployment in difficult terrain, such as humid forest. The solid-state onboard video recording provides substantially improved footage quality over wireless video transmitting devices used previously (Rutz et al., 2007; Bluff & Rutz, 2008), this is due to uninterrupted video with lower levels of visual noise, and no radio-static noise caused by a poor reception. Total video recovery per deployment was also substantially improved over previous units, demonstrating longer runtimes and favourable unit recovery rates. During this pilot study a number of potential design weaknesses were addressed, resulting in even greater recovery success, which could facilitate nearly total rescue rates. Future deployments in difficult humid forest terrain should benefit from these advances.

A number of surprising observations were caught on film during this study. Most notably, two instances of hook-tool manufacture were recorded from two different individuals. We had previously assumed that the crows at our dry-forest site did not use or manufacture hook-tools. This assumption was based on over 800 man-hours of radio-tracking from 2005-2007 (by myself, Lucas Bluff and Christian Rutz), 193 tools recovered from larva-fishing sites (Bluff et al., 2010b), previous crow-cam deployments (Rutz et al., 2007) and extensive hide observations (see chapter 4). These previous lines of investigation also led us to believe that the main mode of tool-use for the crows at our study site was Cerambycid larva fishing; however, my new data suggest paperbark foraging is their primary mode of tool-use, and that hook-tools are manufactured for this role. Although crow-cam footage reveals probing in candlenut deadwood for larvae, and on the ground, the majority of tool-use was directed at paperbark crevices and holes. This helps shed important light on a puzzling conclusion of our previous study that inferred the nutritional dependence of NC crows on tool-use, based on isotopic signatures (Rutz et al., 2010, Rutz et al. in press). Bayesian modelling of likely food consumption rates suggested crows were consuming larvae at a rate considerably higher than we would predict from video-based evidence (Bluff et al., 2010b). We attributed these discrepancies to: (i) underestimating larva intake rates in field observations, (ii) temporal differences in intake rates between field observations and isotope analyses (e.g. fewer larva-fishing sites were active during field observations), (iii) Bayesian energy-budget models erroneously overestimating intake rates, (iv) overestimation of daily metabolic energy consumption of NC crows, which is plausible given their terrestrial foraging lifestyles (Rutz et al., 2007), and/or (iv) failure to identify a food source with a similar ^{15}N-depleted isotopic signature, which is only likely to be found in other wood-consuming animals. My data suggest invertebrates acquired through paperbark foraging (both with and without tools) may explain this missing food source, supporting our assumption (Rutz et al. in press) that this isotopic signature is dependent – to an extent – on tool-use. Although my estimates of tool-use foraging type proportions cannot be directly compared with the Cerambycid larva intake rates calculated in Rutz et al. (2010) because active candlenut foraging sites vary substantially over time as new trees succumb to the larvae and old ones degrade, the evidence I have presented here fills an important gap in our knowledge of the tool-use ecology of marked NC crow population, highlighting the value of animal-borne cameras when studying such an elusive species. The prominence of paperbark foraging in our focal population also conflicts with our previous hypothesis (Rutz et al., 2010) that the anthropogenic introduction of candlenut trees was likely to have prompted the recent (<5000 years ago, see section 1.2) and rapid evolution of tool-use in NC crows, instead demonstrating the greater significance of a native tree species to their tool-based foraging.

3.5.1 Future Research

Future research using biologging-tags will benefit from the continuing drive for small, low-power consumer electronics. I believe the most significant progress in this area will come from miniature embedded PCs. Projects such as Raspberry Pi (www.raspberrypi.org) promise exceedingly cheap (£15) embedded linux computers based on low-power-consuming ARM processors. These units will easily accept almost any data-collection module through standard USB port protocols (such as accelerometers, cameras, GPS units) and further input/output lines for other functions. Most importantly, designers will be able to use simple high-level programming languages to control these units in the same way as a desktop computer for rapid prototyping and deployment. On-board WiFi networking will enable easy data recovery in the field, either through dedicated sink units (i.e. computers left in the field that download any available data from nearby tags wirelessly), or by tracking down animals as they rest and downloading data from a safe distance (20-100m) manually. Wireless download protocols are already implemented in GPS tags, for example, download via ARGOS satellite, GSM (mobile phone networks), or duplex radio (VHF or UHF; however, these solutions are currently too heavy for deployment on most bird species, are very costly, and hypothetical video download speeds would be prohibitively slow and/or expensive. Wireless data downloads also dispense with the need to recover units, so they could be designed for long-term deployment, powered by solar energy from thin-film or third-generation photovoltaic cells.

4 CHAPTER FOUR – FISHING OR HOOKING? THE PROBING STRATEGIES USED BY NEW CALEDONIAN CROWS

4.1 Introduction

Cerambycid larva extraction is an important and well documented form of tool-use in new Caledonian crows, offering substantial energetic rewards to proficient tool-users who can overcome the larva’s inaccessibility (Hunt, 2000b; Bluff et al., 2010b; Rutz et al., 2010). Although my discoveries based on crow-cam observations highlight the significance of paperbark-tree foraging, Cerambycid larvae remain a nutritionally significant and sought-after prey in our dry-forest population (Bluff et al., 2010b; Rutz et al., 2010). Monitoring of marked individuals at Cerambycid foraging sites highlighted the substantial difference in larva extraction proficiency between adults and juveniles (Bluff et al., 2010b). However, this study could not determine whether foraging success in younger crows was limited by their ability to *locate* larvae, or by their ability to *extract* larvae. Other studies observing this behaviour did not provide crows with ecologically relevant extraction tasks, limiting the ecological and behavioural inferences which could be drawn (Hunt, 2000b; Hunt et al., 2006). I therefore set out to investigate the difficulties presented during larva extraction, examining whether this could account for the long learning period required before crows become proficient larva-extractors (Bluff et al., 2010b).

Laboratory studies have highlighted NC crows’ ability to adapt their tool-use behaviour in response to a specific task, for example, choosing tools of an appropriate length (Chappell & Kacelnik, 2002) or diameter (Chappell & Kacelnik, 2004), spontaneously bending or unbending tools in order to make them functional (Weir et al., 2002; Weir & Kacelnik, 2006), and successful meta-tool-use (i.e. using tools in order to retrieve tools) (see section 9.2.5; Wimpenny et al., 2009; Taylor et al., 2010a). The flexibility demonstrated in these studies could suggest that NC crows possess a degree of causal understanding enabling them to mentally simulate a task before performing it (Povinelli, 2000). However, field studies have been less successful in demonstrating this ability: when wild crows were presented with a tool length task they initially probed with a ‘default’ length tool (i.e. a tool length that they would typically forage with), and would only select a longer tool if this failed, implying they adopted a heuristic rule for tool selection (Hunt et al., 2006). Another study testing for wild NC crows’ causal cognition found they were unable to flip pandanus leaf tools so that the barbs became functional hooks; instead, the authors suggest the crows simply follow a specific sequence of stereotyped actions when manufacturing pandanus tools that results in a correctly oriented, functional hook tool (Holzhaider et al., 2008).

Figure 4-1. Cerambycid larva biting onto the tip of a tool with its powerful mandibles (left). The larva in this example is fairly small – approximately 5g – whereas they can grow to 20g or more (pers. obs.). A New Caledonian crow with a larva in its bill (right). A single average-sized larva would provide approximately 6% of a crows' daily energy requirement (Rutz et al. 2010).

Larva 'fishing' exploits the innate behaviour of the prey organism to facilitate its own extraction (see Figure 4-1), as the crows agitate the larva and encourage it to bite onto the end of the tool with its powerful mandibles (Hunt, 2000b). This form of prey-assisted tool-use behaviour is found in chimpanzees exploiting the defensive behaviour of social insects during termite fishing and ant dipping, or relying upon the inherent stickiness of honey during honey dipping (Whiten et al., 1999). The blond capuchin *Cebus flavius* has also recently been found to use stick tools to fish for termites in arboreal nests (Souto et al., 2011). Other forms of probing tool-use exploit the prey's escape response, such as chimpanzees using probes to flush squirrels from holes (Huffman & Kalunde, 1993) or using 'spears' to kill lesser bushbabies (*Galago senegalensis*) to prevent them escaping (Pruetz & Bertolani, 2007), and NC crows using tools to flush lizards from holes (chapter 2; Troscianko et al., 2008). Another, potentially passive, form of tool-use may not rely on the prey's behaviour to assist extraction, for example woodpecker finches using cactus spines to spear or lever prey from inaccessible crevices (Tebbich et al., 2002), or NC crows using barbed pandanus tools and hooked-stick tools to extract inaccessible invertebrates (see section 1.2; Hunt, 1996; Hunt & Gray, 2004a).

Cerambycid larvae burrowing through deadwood present a unique and interesting model system in which all three of the probing mechanisms outlined above could be used in different circumstances. As the deadwood erodes, new sections of the complex burrow system are exposed to NC crow foraging; in many cases the larvae will be in a burrow facing towards the crow so that they can be fished out. However, when the larvae are encountered facing away from the crow they could either exploit the larva's escape response – herding it through an open-ended burrow and out of another hole through the log – or must hook it from the burrow unassisted (independent of prey behaviour). I have based my study on this system to investigate whether NC crows can flexibly adopt different tool-use strategies dependent on the context provided by the orientation of the prey and to model the extraction techniques they use.

I presented wild NC crows with a tool-use task mimicking Cerambycid larva extraction in the wild; larvae were offered in artificial holes with hidden cameras filming the larva-tool interaction from within the 'larva-cam' log. Larvae were oriented either with their mandibles up, or down, simulating two scenarios that wild NC crows are likely to encounter and their tool-movements were tracked in order to examine the probing strategies used in each situation.

4.2 Methods

Two larva-cam units were deployed in successive field seasons. The first unit, deployed in December 2007, was constructed from a large round plastic container clad with bark and topped with frass (the sawdust-like waste produced by burrowing Cerambycid larvae) which resembled an candlenut tree (*A. moluccana*) buttress. The surface contained ten holes of 20mm diameter, below each of which a Pyrex™ test-tube (of 19.8mm internal diameter) was suspended. An infrared panning camera within the unit could be controlled remotely from the hide to view and record the activities within any one of the eight test-tubes accessible to its 300° panning mechanism. The second larva-cam unit, deployed in January 2009, was constructed from a hollowed out section of candlenut tree trunk approximately 100cm long and 25cm in diameter placed on its side with a single 25mm hole in the upper surface (Figure 4-2A). Larvae were presented in a Perspex tube with a diameter of 25mm. An infrared video camera was hidden within the log and two mirrors were positioned either side of the tube to grant a full 360° view around the tube, eliminating blind spots behind the larvae (Figure 4-2B).

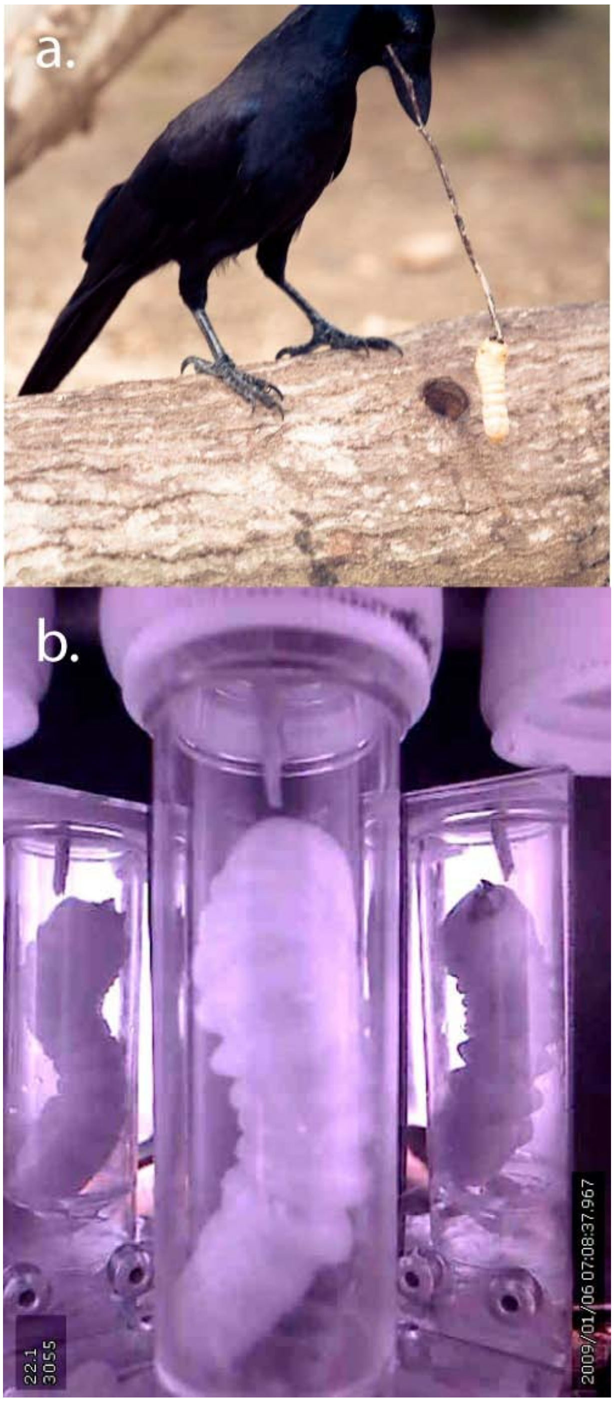

Figure 4-2. (a) Photograph of an unmarked crow ‘fishing’ a larva from the second larva-cam log. (b) Still frame of larva-cam footage; the larva is positioned mandibles-up, shown interacting with a tool-tip. Two mirrors behind either side of the central tube provide an uninterrupted view of the tool-tip and larva from all around.

The larva-cam units were positioned in Gouaro-Déva, our dry-forest study site on Grande Terre at coordinates -21.556246°S, 165.315458°E. Experimental larvae were collected periodically from three locations >1.5km from the experimental site. Larvae of all weight ranges were used to pre-bait the first larva-cam unit daily, for 30 days. All ten tubes were baited with five larvae oriented mandibles-up and five down, allocated randomly to a given tube. A motion-triggered video camera monitored the pre-baiting process in order to identify wing-tagged crows using the site. The second larva-cam unit was positioned within 15m of the first unit the following year without pre-baiting, but following another experiment at the same site that involved wild NC crows extracting pieces of meat from holes in a solid log of similar dimensions to the second larva-cam unit.

The first larva-cam experiment ran throughout December 2007. Larvae between 3 and 5 g were presented in one of the eight holes visible to the camera (chosen randomly) in a pseudo-randomised orientation, which randomised larva orientation evenly in blocks of 8 trials. This weight range was chosen to exclude larger larvae that could wedge themselves in the bottom of the tube, and smaller larvae that could flip their orientation. Larvae in the experimental weight range could still flip their orientation, but did so rarely and in both directions: trial orientation was determined by the larva's orientation at the start of each trial. Immediately prior to each trial larvae were weighed on portable digital scales (0.01g precision) and morphometric measurements were made with digital callipers to a precision of 10^{-5} m including: mask width, mask height and mandible length. Prior to each trial all potential tool materials were cleared from a 1m radius of the larva-cam unit to assist tool retrieval. The second larva-cam experiment was run throughout January 2009; larvae >6g were positioned in a pseudo-random orientation in the tube.

All crow activity was videoed from the hide and larva-cam filming commenced when a tool-carrying crow approached the unit. Unmarked individuals were identified from their unique leg-scale and leg scarring patterns that were photographed from the hide with a 400 mm lens and digital SLR camera. Both unmarked individuals had specific patterns on their legs visible when magnified from high-definition photographs in the field. A variety of differences allowed me to differentiate between individuals, such as the presence of small depressions in their legs and the relative positioning of these depressions to the edges of leg scales. This method permitted identification of individuals in previous trials (i.e. before the individual patterns were distinguished), and could also be independently verified across a daily/weekly timescale using additional individual information such as moult condition (e.g. on the wing covets). A trial would start when a crow inserted a tool into the unit and would finish when the subject flew away beyond sight from the hide and did not return for 5 minutes. Larvae would rarely survive a trial, generally being extracted, pierced and killed, or otherwise injured, so were replaced even if they appeared unharmed. Following a trial all tools used were recovered where possible (i.e. when the crow did not fly away with a tool) and a new trial was prepared to start 10 minutes later.

A trial started when a crow approached the experimental apparatus with a tool, and ended five minutes after the subject left the area (>25 m away). Larva-cam video footage was used to determine the method of extraction as either ‘fishing’ (i.e. the larva held onto the tool with its mandibles during extraction), or ‘hooking’ (i.e. the larva was drawn up without facilitation from biting). Manual frame-by-frame video analysis was used to track the position of the tool tip while the crow was probing (ImageJ, version 1.42). Lens distortion and perspective were modelled from calibration data gathered for each tube so that the tool tip’s depth could be accurately calculated from pixel coordinates on each frame. Calculations were performed using Microsoft Excel 2007. For each trial, all upwards tool movements were pooled and averaged, then the average of all trials was used for the overall average upwards tool movement. The same procedure was used to calculate the average downwards tool movement. These values were subsequently used for categorisation of tool movements in each frame of tracking as either faster or slower than the relevant upwards or downwards average. For each trial the number of fast and slow tool movements in upwards and downwards directions was tallied to create a proportional binomial response variable for each trial. The average tool depth was also calculated as the mean of pooled trial mean tool depth values. The average depth was used to compare tool movements in the lower (< mean depth) and upper (>mean depth) portion of the tube in order to determine whether the observed effects could be attributed to mechanical factors arising from changing larva orientation; for example, when oriented up, the chitinous head of the larva may act as a greater obstruction to tool movement than the soft, narrower tail of larvae oriented down. Feedback events were identified as instances where the larvae were drawn >20mm up the tube in a short timeframe (<5 frames) without successful extraction. Only the first feedback event of each trial was considered, and each was classified as 'fishing' or 'hooking'. A proportional binomial response variable was calculated from the number of faster than average upwards and downwards tool movements in the 200 frames preceding the feedback event compared to the number in the subsequent 200 frames. Feedback events without the full 400 frame window of tool-tracking were discarded.

All statistics were performed using R, version 2.11.1 (2010-05-31) (R-Development-Core-Team, 2011). Generalised linear mixed models (GLMMs) were executed using the lme4 package, version 0.999375-35 (2010-08-18). Mixed models are able to handle random and fixed variables in the same model, nesting of random factors, and repeated measures that can, for example change over a sequence. GLMMs are therefore more appropriate than standard parametric regressions such as GLMs for behavioural data where subjects are necessarily random factors. In all models crow was treated as a random effect on the intercept, and trial number was treated as a random effect on the slope (Crawley, 2007). Where the effect of trial number explained little of the variance of a model it was eliminated, and if the subsequent model had a lower AIC the simplified model was accepted (Crawley, 2007). Residuals were checked for conformity of data to model assumptions by fitting the data to GLMs (Bolker et al., 2009). GLMMs with a Gaussian (normal) response variable were fitted using the REML algorithm, while binomial response variables were fitted using Laplace (Bolker et al., 2009). Confidence intervals and P-values could be generated from lme4 REML-fit models by using a Markov chain Monte Carlo (MCMC) method implemented using the languageR package version 1.0 (2010-06-04), using the pvals function with 10,000 model iterations (Baayen et al., 2008), but only in models where trial number could be legitimately eliminated (based on AIC values), because this method does not currently support more than one random effect.

4.3 Results

Data were collected from three crows across 92 trials, yielding a total of 200,706 tool tracking points, for a summary of trial data see Table 2, Figure 4-3 shows example tool traces. One unmarked wild crow ('UC1') participated in trials with the first larva-cam unit, completing 26 trials. Two further crows participated in trials with the second larva-cam unit. The first of which was an unmarked individual ('UC2') which was observed to have a pink gape consistent with it being approximately one year old, this individual completed 50 trials; the second was an individual marked with wing-tags and rings as part of our ongoing trapping program, identified as HM2. HM2 completed 16 trials. All three individuals encountered larvae presented up and down, and all used fishing and hooking methods to retrieve larvae (see Table 2 for summary statistics).

	Crow ID			
	UC1	UC2	HM2	Total
Total trials	26	50	16	92
Abandoned	14	14	3	31
Fished	7	24	7	38
Hooked	5	12	6	23
Larvae up	11	19	7	37
Larvae down	15	31	9	55

Table 2. Summary of trial numbers, outcome and larva orientation.

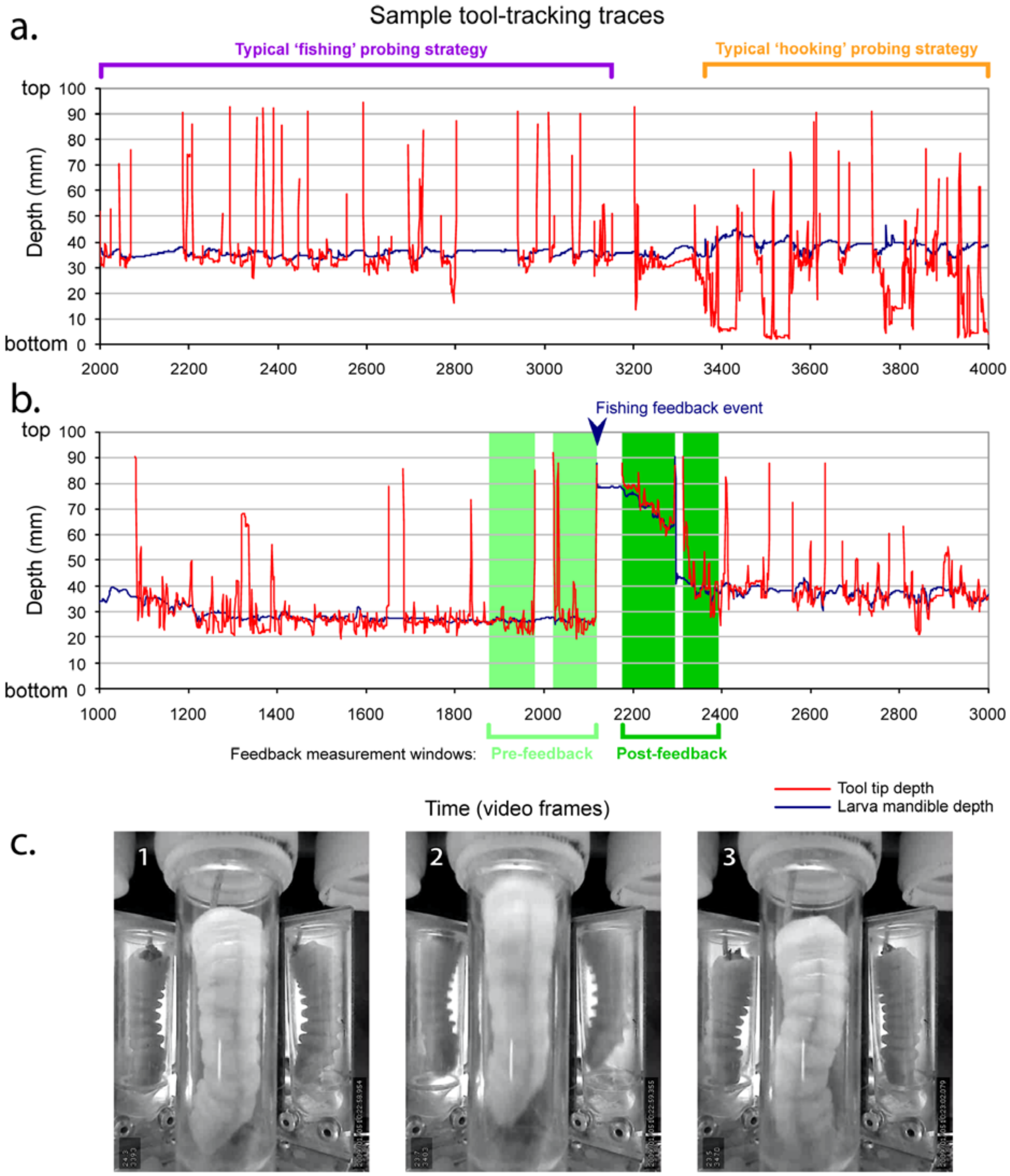

Figure 4-3. Sample tool-tracking traces (red) and larva mandible traces (blue). Typical fishing and hooking probing strategies are shown where a crow switches from one strategy to the next in this snapshot of a single trial (a). Below this a fishing feedback event – where the larva is nearly extracted – is arrowed (b), and the 200 frame windows before and after the event are shaded green (the gaps in these windows are due to the tool being withdrawn from the tube). Panel c shows film stills showing (1) a larva biting onto the tool-tip, (2) the larva being drawn upwards, and (3) the larva having fallen back down to the base of the tube after letting go of the tool.

Larvae were more likely to be extracted when oriented up (t=-4.99, *P*<0.001), and trials were significantly shorter when larvae were 'fished' out as opposed to 'hooked' out (t=-3.44, *P*=0.001). There is no evidence to reject the null hypothesis that there is a difference in trial length between trials in which larvae were 'hooked' out and abandoned trials (t=-1.27, *P*=0.206). Amongst all successful trials, larvae were more likely to be 'fished' out when oriented up and 'hooked' out when oriented down (z=-4.58, *P*<0.001). From a total of 61 successful extractions, when oriented up, 4 larvae were hooked out, whereas 32 were fished out. When oriented down, 19 larvae were hooked out, while 6 were fished out. Average tool depth was significantly influenced by an interaction between larva orientation and larva weight (t=2.27, *P*=0.026). Overall, there is a positive correlation between larva weight and average tool depth (i.e. the tool tip was on average deeper when larvae were lighter and higher when larvae were heavier), when larvae are oriented up the average tool depth was higher, and the positive relationship between larva weight and average tool depth was increased. Average upwards tool movements were 4.51mm per frame, and average downwards tool movements were 4.46mm per frame. Larva orientation and weight interacted to significantly affect the number of fast versus slow upwards (z=-13.93, *P*<0.001) and downwards (z=-10.56, *P*<0.001) tool movements. When larvae are oriented up there was a negative correlation between the frequencies of fast upwards and downwards tool movements and larva weight (e.g. slower tool movements were used with heavier larvae). Conversely, when larvae were oriented down there was a positive correlation between the frequencies of fast upwards and downwards tool movements and larva weight (e.g. faster tool movements were used with heavier larvae see Figure 4-4). When these data were analysed to examine the tactics used by each individual there was one instance where this overall trend was not followed clearly: when larvae were oriented down, crows UC2 and HM2 responded positively to larva weight, using faster tool movements with heavier larvae, while UC1 exhibited a weaker response to larva weight, using slightly slower movements with heavier larvae. Across all GLMMs trial-number explained very little of the observed variation, and the AIC was lower when this was removed from the models, indicating the crows did not improve or change their strategies throughout the course of the experiment.

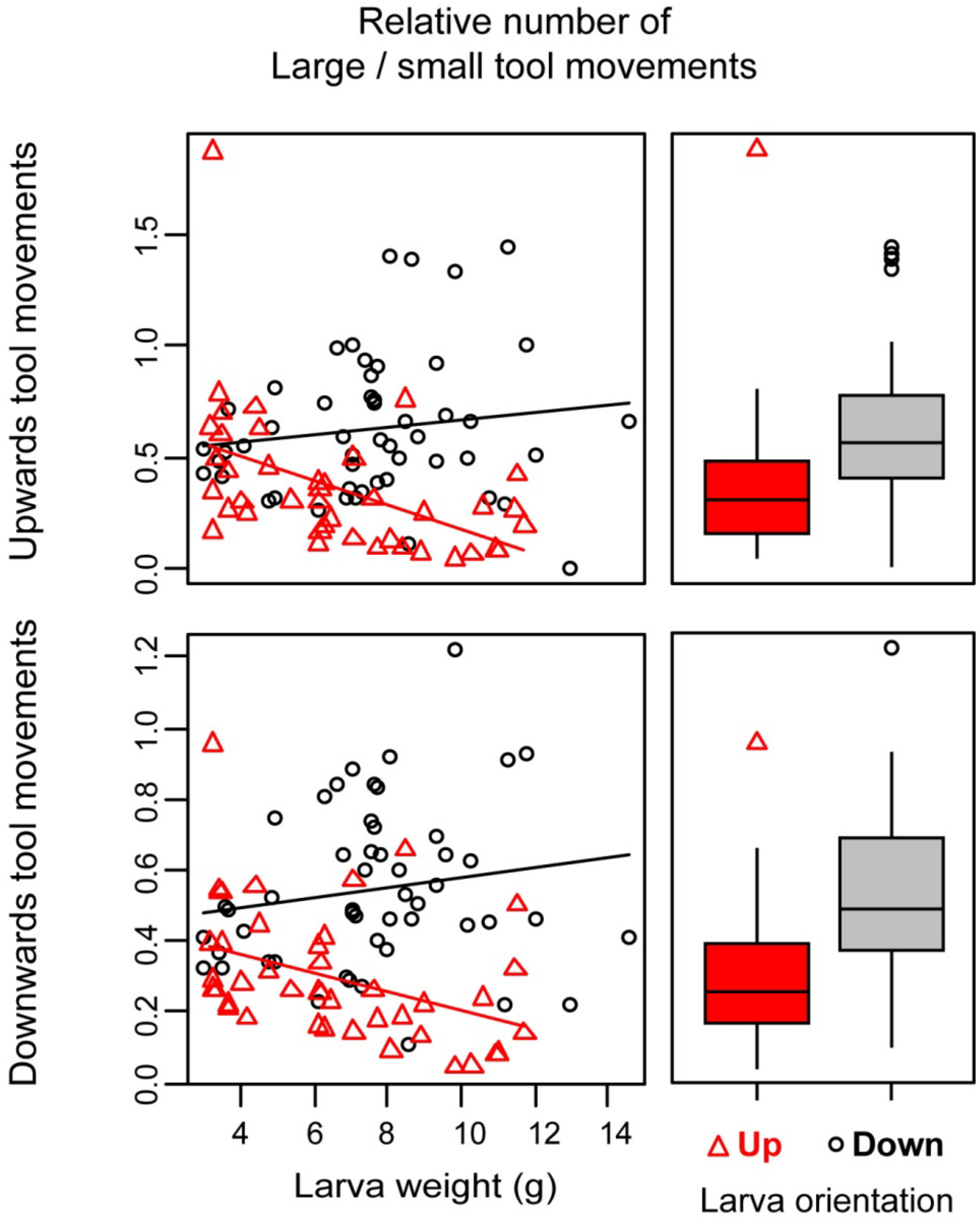

Figure 4-4. Larva-cam average trial data. Scatter plots on the left show the magnitude of average upwards and downwards movements when larvae were oriented up (red) or down (black), with larva weight shown on the x-axis. The difference in orientation between these regression lines illustrates the clear interaction between larva weight and orientation on the number of large tool movements. Box-plots on the right (using the same y-axis scale as the scatter plots) show that overall, there were significantly more frequent upwards and downwards tool movements when larvae were oriented down (boxes show median and interquartile ranges, plus individual outliers).

A total of 28 feedback events were identified from all three crows, 18 of which were hooking events and 10 fishing. Following a hooking event the mean number of larger than average upwards tool movements increased significantly from 28.2 to 37.7 over the 200 frame windows, while the mean number following a fishing event remained unchanged from 15.3 to 15.7 (z=-2.6, *P*=0.001). There is also some evidence for an interaction between larva weight and feedback type, with a greater number of faster than average upwards tool movements being used following a fishing event with larger larvae (z=1.9, *P*=0.060). Analysis of larger than average downwards tool movements shows no significant change following a feedback event in relation to the type of feedback (z=-1.6, *P*=0.115), however, there is some evidence for an interaction with larva weight (z=1.9, *P*=0.061). Orientation and feedback type are highly confounded; this is to be expected given the tendency to hook larvae out when they are oriented down, and to fish them out when oriented up. See Figure 4-5 for data.

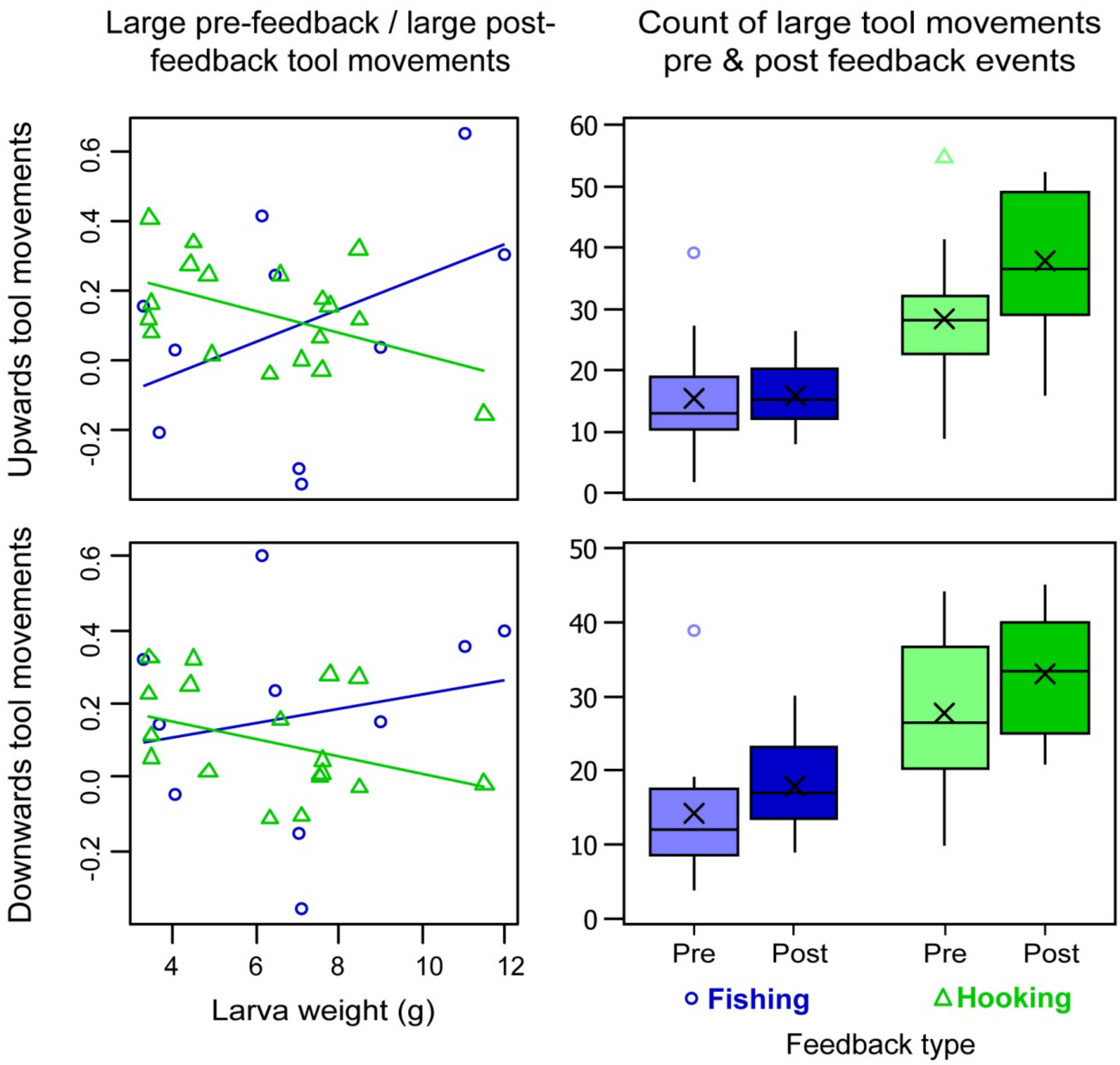

Figure 4-5. Feedback event data. Scatter plots on the left show the (nearly) significant interaction between larva weight and probing tactic on the number of large tool movements. Box-plots on the right show the total number of counts of larger than average tool movements in the 200 frames preceding and following feedback events. Notice that while hooking, there are generally far more large movements, and that there is a significant increase following a hooking event, but not a fishing event (boxes show median and interquartile range, crosses show mean values, plus individual outliers).

4.4 Discussion

Wild New Caledonian crows are able to flexibly adapt their tool-use behaviour dependent on context. When larvae are oriented up the crows gently tease them, targeting their mandibles in an attempt to coerce them into biting onto the end of the tool, a strategy consistent with the ‘fishing’ behaviour described by Gavin Hunt (2000b). I also demonstrated the use of a second probing strategy when larvae are oriented down, characterised by faster tool movements along the entire length of the tube. This behaviour is consistent with a ‘hooking’ strategy (see Figure 4-3), which crows are forced to adopt when the larva’s mandibles are inaccessible. Additionally, I found that NC crows were sensitive to the weight of the larvae and to fishing or hooking events that nearly resulted in successful extraction. The crows used faster upwards tool movements on larger larvae following an instance where the crow experienced the larva biting onto the tool. Larger larvae would not only have a more powerful bite with which to grip the tool, but were better able than smaller larvae to wedge themselves against the walls of the tube, requiring a greater force to extract them before they open their mandibles again. Following the first fishing feedback event a crow would have been able to judge the force with which the larva resisted extraction, and my data suggest the crows were sensitive to this information and immediately adjusted their tool-use behaviour appropriately. Following instances where the larva was drawn up the tube by hooking without successful extraction the crows immediately began using frequent fast upwards tool movements, likely to replicate the previous hooking event. I found no evidence of tool selectivity or hook-tool manufacture and use; all tools used were stick tools (without hooks), or candlenut leaf stems (which can have a semi-hooked lobe at the abscission layer). It is noteworthy that none of the three individuals attempted to make or use hooks when larvae were oriented down. We still know very little about hooked tool-use in our focal population; with just two confirmed instances captured by my recent crow-cam deployments (see chapter 3) we cannot determine the frequency or distribution of hook-tool manufacture and use.

New Caledonian crows exhibit an inherited propensity to use and manufacture tools in captivity (Kenward et al., 2005; Kenward et al., 2006). The ontogeny of tool-use behaviour in hand-raised individuals reveals a number of ‘precursor actions’ used to manipulate objects before demonstrating mature tool-use. These include behaviours such as poking or rubbing surfaces with a stick, or proto-probing, i.e. holding a stick in the bill and moving it backwards and forwards in a similar manner to probing, without insertion into a hole. The acquisition of tool-use behaviour, therefore, appears to rely on genetically-determined developmental steps, including motor schemes that emerge before functional tool-use (Kenward et al., 2006), and a recent study suggests this could have developed from caching behaviour ancestral to all *Corvus* species (Kenward et al., 2011). Social learning was not found to be necessary for successful adult tool-use to manifest, but those hand-raised crows that were given the chance to interact with human tool-using demonstrators acquired the behaviour faster. This ontogeny shares parallels with the tool-using Galapagos woodpecker finch, which passes through a number of key stereotyped developmental stages before using tools, such as ‘uncoordinated manipulations’ (Tebbich et al., 2001, p.2192) and ‘exaggerated, playful movements’ (p. 2191) while holding twigs. Similarly, social learning was not found to be necessary for tool-use acquisition, instead the provision of raw tool materials and probing opportunities was sufficient for the behaviour to manifest (Tebbich et al., 2001).

The dependence of tool-use behaviour on inherited precursor actions has led some to argue that tool-use may be under the same tight genetic control as nest building, and that the cognitive demands of tool-use are no more sophisticated than those used by a bird when constructing a complex nest from a diverse range of materials (Hansell & Ruxton, 2008). The ability of a tool-user to flexibly modify a tool prior to use has been cited as evidence to counter this argument, examples include woodpecker finches removing side-braches on tools that would prevent insertion (Eibl-Eibesfeldt, 1961; Tebbich & Bshary, 2004), and chimpanzees 'crafting' spears using a non-predetermined sequence of steps thought to 'involve the kind of foresight and intellectual complexity that most likely typified early human relatives' (Pruetz & Bertolani, 2007 pp.414). However, Hansell and Ruxton (2008) point out that the lack of stereotypy in these cases could be compared with that shown by some spiders during web construction, for example, linyphiid and theridiid orb-weaver spiders, which are able to reverse significant stages of web construction in a flexible manner (Benjamin & Zschokke, 2004). In this study I show NC crows are also able to flexibly modify their tool-use behaviour, but in order to determine whether this behaviour is stereotyped, or governed by inherited rules we must investigate how the behaviour develops.

Although the set of rules necessary to exhibit distinct fishing and hooking larva extraction strategies could theoretically be genetically predetermined, the long period of time taken to become a proficient larva-extractor suggests an extensive learning period is required. Hand-raised NC crows started to insert sticks into holes using highly stereotyped actions from approximately 4-8 weeks old (Kenward et al., 2006), however, evidence from field studies suggests NC crows continue to use tools with little success for perhaps 2 years, long after the stereotyped precursor actions have established adult-like tool-use (Bluff et al., 2010b; Holzhaider et al., 2010a). Motion-triggered video observations of wild, marked individuals using tools at our study site highlight the persistence with which young crows probe unsuccessfully; in one instance an immature crow probed for 3 hours without success, and another probed for 5 hours with just one successful extraction. Meanwhile, proficient adults extracted larvae far more efficiently from the same foraging sites (Bluff et al., 2010b). Additionally there is evidence that NC crows' social structures permit immature crows to remain a part of the family unit for over two years, and an immature adult may continue to be fed by its parents during this time (Holzhaider et al., 2011), suggesting any costs associated with long tool-use development periods are a burden to the parents as well as the juveniles. Genetically-determined or stereotyped behaviours permit an animal to perform complex and sometimes flexible actions with little or no prior experience – such as constructing complex nests or spider webs. In contrast, young NC crows and their parents apparently invest heavily in a lengthy period of non-stereotyped tool-use characterised by low extraction rates in order (presumably) to profit from it later in life, probably motivated through internal reward (e.g. Deci & Ryan, 1985 pp. 32-48). It therefore seems unlikely that the hooking and fishing behaviours we have characterised are under tight genetic control, suggesting the behaviour is honed through individual learning, social learning, or mental simulation of the causal properties of the task.

Certain aspects of larva-fishing could be learnt socially; for example, local or stimulus enhancement could foster selection of a suitable burrow or tool. The nature of larva-fishing, however, makes it extremely difficult for one crow to observe the probing behaviour of another in response to the condition of the prey, as exemplified by this study, which required cameras hidden within the log and fine-scale analysis of the tool movements. Therefore it is unlikely social learning (whether that be local/stimulus enhancement, emulation or imitation) could account for the distinct fishing and hooking strategies used by NC crows alone. Equally, we cannot rule out the possibility that the crows take time to develop an understanding of the causal principles governing Cerambycid larva extraction, and that they use this understanding to respond to the different affordances presented by larvae in either orientation. There is little evidence to suggest NC crows have a qualitatively different form of tool-oriented cognition from their relatives, as a recent study found non-tool-using rooks (*Corvus frugilegus*) were able to use tools in a number of sophisticated tasks (Bird & Emery, 2009a) (although see section 9.2). Instead, I believe the most parsimonious explanation is that lengthy periods of individual trial and error learning are required to perfect the technique for extracting larvae (see Bluff et al., 2007). This hypothesis would predict that different individuals would slowly develop and settle upon slightly different strategies, and we do find evidence that the youngest crow in this experiment (as gauged by the proportion of pink in its gape), did not respond to larva weight as readily as the older individuals. However, a larger sample size across a developmental cross-section would be required to investigate the ontogeny of larva extraction strategies and the precise nature of the learning mechanisms used.

Extracting wood boring larvae from their heavily protected burrows armed with nothing but a small stick is a difficult task. Furthermore, the nature of the task shifts markedly depending on the orientation of the larva, from a test of subtlety and coercion when the larva is able to bite onto the tool tip, to one of speed and force when a larva is facing away from the tool and must be hooked out before it can crawl to safety. Here I have demonstrated how New Caledonian crows adopt different extraction tactics dependent on larva orientation, and have shown how they are able to adjust their behaviour in response to feedback from the larva and the size of the reward. Such responsiveness to the affordances of the larvae appears to take a great deal of time and energy to acquire, presumably partly through individual trail-and-error learning. These inherent costs of tool-use mean that under stable environmental conditions it would probably not compete favourably with the morphological specialisations for larva-extraction seen elsewhere in the world, perhaps helping to account for the scarcity of tool-use in the animal kingdom.

4.5 Further Research

My findings highlight NC crows' sensitivity to feedback from larvae while probing, but the larva-cam study was unable to determine how crows gauged the larva's size and behaviour. Touch (combining pressure sensing and proprioreception) and vision are likely to be the most important sources of information during tool-use, and experimental manipulation of the visual and tactile cues could establish the primary sensory mode NC crows rely on while probing. I attempted to manipulate the visual cues presented by larvae in the larva-cam apparatus by painting the face-masks of some larvae with a pale, body-coloured paint, and gluing moulted masks to the tails of larvae in order to assess whether this is sufficient to switch their probing strategy from fishing to hooking or vice-versa. Although I was unable to successfully manipulate these cues due to material technicalities, the larva-cam experiment (chapter 4) showed that NC crows tend to visually inspect holes before locating a tool and probing, suggesting vision at least plays a major role in identifying suitable burrows. However, maintaining visual contact with a tool while probing may be problematic for NC crows due to the close and inflexible mechanical coupling of their eyes and the tool held in their bill when compared to the mechanical flexibility of primate tool-users. Tool-use in humans relies heavily on visual perception and dextrous, sensitive hands but these potential prerequisites for human-like tool-use in other animals have been almost entirely overlooked in comparison to the considerable focus on cognitive explanations for tool-use.

5 PART TWO – MORPHOLOGY

5.1 Introduction

Humans make and handle tools with a proficiency unmatched by any other animal. We possess several morphological features that allow us to deploy tools with ease; our dextrous hands and uniquely opposable thumbs allow us to manipulate objects with strength and precision (Napier, 1962; Susman, 1994), and our visual system can guide our movements using accurate relative depth perception (Foley, 1980). Yet research has almost exclusively focused on cognitive differences between humans and other tool-using animals and no other habitual tool-users are known to benefit from similar morphological adaptations. So far I have addressed some of the ecological features that might account for tool-use in New Caledonian crows. Here I shall address the role of their morphology before considering cognitive abilities in the last part of my thesis. First, I review the current evidence for morphological/anatomical adaptations relating to tool-use in the NC crow, and compare this to primates and hominids; I then present my evidence for tool-use specific morphology in NC crows.

5.1.1 *Dextrous Tool-use*

The Human hand can hold and manipulate objects with a degree of precision and flexibility surpassing that of any other animal, including our closest living relatives. John Napier (1956) first highlighted the two discrete forms of grasping movements unique to human hands: the precision grip and power grip. Soon afterwards the fossilised remains of *Homo habilis* were unearthed alongside the earliest stone tools in the Olduvai Gorge, and Napier (1962) concluded that the hand of this hominid would have supported tool-use facilitated by basic power and precision grips. Subsequent hominid fossil finds have fuelled the debate over the timing and significance of morphological aspects of the hand adapted for tool-use. Amongst the most important features identified are: (i) Fully opposable thumbs controlled by a proportionately large flexor pollicis longus muscle and well developed tendon; (ii) relatively long thumb and short fingers to facilitate the precision grip; (iii) wide, fleshy thumb and fingertips that maximise surface for friction thanks to broad ungula tufts; (iv) Flexible wrists that permit the precision grip to be used at a range of angles (e.g. see: Susman, 1994; Susman, 1998; Marzke & Marzke, 2000). These modest, yet important features are the only clear morphological adaptations for tool-use in the animal kingdom, but in humans these anatomical attributes are also combined with a level of fine motor control in our hands (dexterity) unmatched by any other tool-user.

The percussion flaking used to manufacture Oldowan stones *c*. 2.5 Ma would have needed relatively precise, well-aimed blows requiring greater dexterity than that used by adult chimpanzees hammering open nuts (Boesch & Boesch, 1990). A bonobo *Pan paniscus* that was intensively trained in stone tool flaking for three years was unable to strike forcefully or at the correct angle and position to make Oldowan-like artefacts (Toth et al., 1993). Adaptations in the primate hand thought to suit arboreal quadrupedal locomotion prevented the bonobo from handling tools with the manual skill of a human hand (Susman, 1998; Ambrose, 2001). The Acheulean hand axes associated with *H. erectus* remains from *c*. 1.6 Mya mark an even more definitive increase in hominid dexterity, requiring precision handling, bimanual role differentiation (each hand performing different but complimentary roles), greater precision aiming of powerful blows, and flexible use of powerful and delicate strikes to prepare the surface or correct errors (reviewed by Byrne, 2004). Strong population biases for right-handedness then manifest in modern humans *Homo sapiens c*. 100,000 to 200,000 years ago, thought by some to demonstrate specialisation of the brain's left hemisphere for greater manual control (Ward & Cantalupo, 1997), and perhaps sequential action planning (Corballis, 1991); although a number of other theories have been proposed, for example, suggesting that the dominance of the left hemisphere is related to our development of language (Deacon, 1997; Corballis, 2003).

There is evidence that great apes possess some of the manual skills thought to be essential for human-like tool-use, including bimodal role differentiation and individual manual laterality (Byrne, 2004). For example, ant dipping chimpanzees at Gombe use one hand to control the tool as ants swarm up it, then with their awkward precision grip they sweep the thumb and forefinger of their other hand along the tool to collect the ants (McGrew, 1974). Some chimpanzee tool-use – such as termite fishing – demonstrates individual lateralisation, and more strongly lateralised individuals extracted termites faster than ambidextrous or weakly lateralised individuals (McGrew & Marchant, 1999). Additionally, a recent study showed that as the physical awkwardness of a task increases, chimpanzees' original handedness biases are reinforced (Braccini et al., 2010). Similarly, gorillas *Gorilla beringei beringei* demonstrate precision bimanual differentiation while overcoming the physical defences of plant food sources (Byrne et al., 2001); they are highly lateralised during feeding (although their handedness in one feeding technique does not predict it for another), and more lateralised individuals prepared food faster (Byrne & Byrne, 1991).

Approximately 90% of humans are right-handed, and while there is some evidence for similar species-wide biases in great apes (Lonsdorf & Hopkins, 2005), there is also no clear evidence of handedness being correlated with any specific abilities in humans (Hardyck & Petrinovich, 1977). Therefore population-wide handedness need not be a prerequisite of human-like tool-use, but could relate to other developmental, social or evolutionary factors. Nevertheless, Hunt et al. claim to find evidence for population-level laterality in NC crows (Hunt, 2000a; Hunt et al., 2001). In an island-wide survey across 19 sites, significantly more pandanus tool counterparts were found on the left edges of clockwise spiralling *Pandanus* spp. trees than the right edges, while there was no difference observed in anti-clockwise spiralling trees. Although Hunt et al. (2001) sampled a total of 3727 counterparts there is no way of telling how many individuals this represents. Indeed, given that *Pandanus* spp. leaves can remain on the plant for four years (Hunt, 2000a), it is feasible that all the tools sampled in a given site were made by one individual crow, or by a small number of closely related individuals. It is also interesting to note that the only NC crow observed to make stepped tools in the wild did so from both left and right leaf edges, but used the tool exclusively with a left-lateralisation. In the laboratory NC crows demonstrate very clear individual laterality, with biases for holding tools against the left or right cheek in 97.7% of tool bouts, however, of the 14 subjects tested half were left-lateral and half right (Rutledge & Hunt, 2004; Weir et al., 2004). This dichotomy in laterality led Weir et al. (2004) to suggest that tool-use and tool manufacture could have different neural bases in NC crows. However, hemispheric specialisation for different visual tasks is common throughout all vertebrates (Rogers, 2002), raising the possibility that NC crow laterality disparity could manifest as a simple response to the differences in visual feedback available while *making* or *using* tools.

5.1.2 Vision & Tool-use

The primate body plan affords a clear view of objects in the hand. Additionally, our binocular, forward facing eyes can provide precise relative depth perception of near surfaces. There are a number of visual cues available to humans to gauge depth, but the parallax between our two eyes can be used to calculate distances accurately without the need for head movements and with minimal surface cues (such as lighting or texture) (Foley, 1980). Some speculate that this binocular vision evolved in primates to provide visual redundancy while peering through dense vegetation (Changizi & Shimojo, 2008) or to boost nocturnal vision (Crompton, 1995), while others argue that stereopsis and depth perception are adaptations for judging distances in arboreal locomotion (Collins, 1921), or to aid inspection and manipulation of items in the hand (Harris, 1953;; reviewed by Heesy, 2009). In contrast, birds have lost the potential to use their forelimbs for object manipulation, limiting them to using a single foot and/or their bill (although Kea and caracaras sometimes lie on their backs while manipulating objects with their bill and both feet, pers. com. Dr. Jackie Chappell & Dr. Auguste von Bayern). Birds' bills and feet are ill suited for combining a powerful, precise grip with visual feedback, and it is these factors of NC crow morphology I shall address in chapter 6, but first I review claims that NC crow neuroanatomy could have changed in response to cognitive and fine motor control of tool-use.

5.1.3 Brain anatomy & tool-use

Cognitive abilities have been found to correlate with total brain size in a number of species (Nicolakakis & Lefebvre, 2000; Lefebvre et al., 2002; Reader & Laland, 2002; Dunbar & Shultz, 2007), and in humans our proportionately large cerebellum – both in comparison to body mass and scaled with cerebral cortex size – may have developed in response to tool-use (Rilling, 2006). Thought by some to act as a modulator of neural activity in connected brain areas, the human cerebellum could improve the processing efficiency and acquisition speed of not only fine motor skills, but also cognitive functions (Snider, 1950; Weaver, 2005). Others suggest that selective pressure to improve throwing ability could account for increased cerebellar volume (Isaac, 1987), and the improved dexterity of humans in comparison to other apes discussed above would support the tool-use hypothesis in addition to the cognitive manual skills proposed by Byrne (2004), such as hierarchical organisation and anticipatory schema.

The flexible behaviour and problem solving skills demonstrated in *Corvus* species has been linked to their relatively large brains (Lefebvre et al., 1997). But has tool-use in NC crows co-evolved with a proportionately larger brain – or proportionately larger brain region – than their non-tool-using relatives, akin to the human cerebellum? Two studies have investigated brain anatomy in NC crows, attempting to test this hypothesis. The first, (Cnotka et al., 2008) asserts that NC crows have an “extraordinarily” large brain in comparison to other *Corvus* species. However, the dataset Cnotka et al. used for their comparison contained only four European *Corvus* species; the common raven *C. corax*, carrion crow *C. corone*, rook *C. frugilegus*, and jackdaw *C. monedula*. Evidence from an earlier dataset (Iwaniuk & Nelson, 2002) suggests that these species have lower brain mass/body mass indices than other members of the *Corvus* genus from the new world. Iwaniuk & Nelson (2002) provide comparable data for two additional *Corvus* species: the little raven *C. mellori* (n=3), and the American crow *C. brachyrhynchos* (n=1). The tissue preparation methods differed slightly between these datasets; Iwaniuk & Nelson fixed the brain in formalin for 1-2 weeks before weighing whereas Cnotka et al. used fresh samples. However, where the datasets overlapped (the common raven and magpie *Pica pica*), both methods reveal almost identical values. Figure 5-1 highlights the observation that the two additions provided by Iwaniuk & Nelson’s dataset have a larger brain mass/body mass index than the NC crow, i.e. they lie further from the regression of all birds than the NC crow. Thus when the American crow and little raven are added to Cnotka et al.’s (2008) analysis there is little evidence supporting their conclusion that NC crows have extraordinarily large brains.

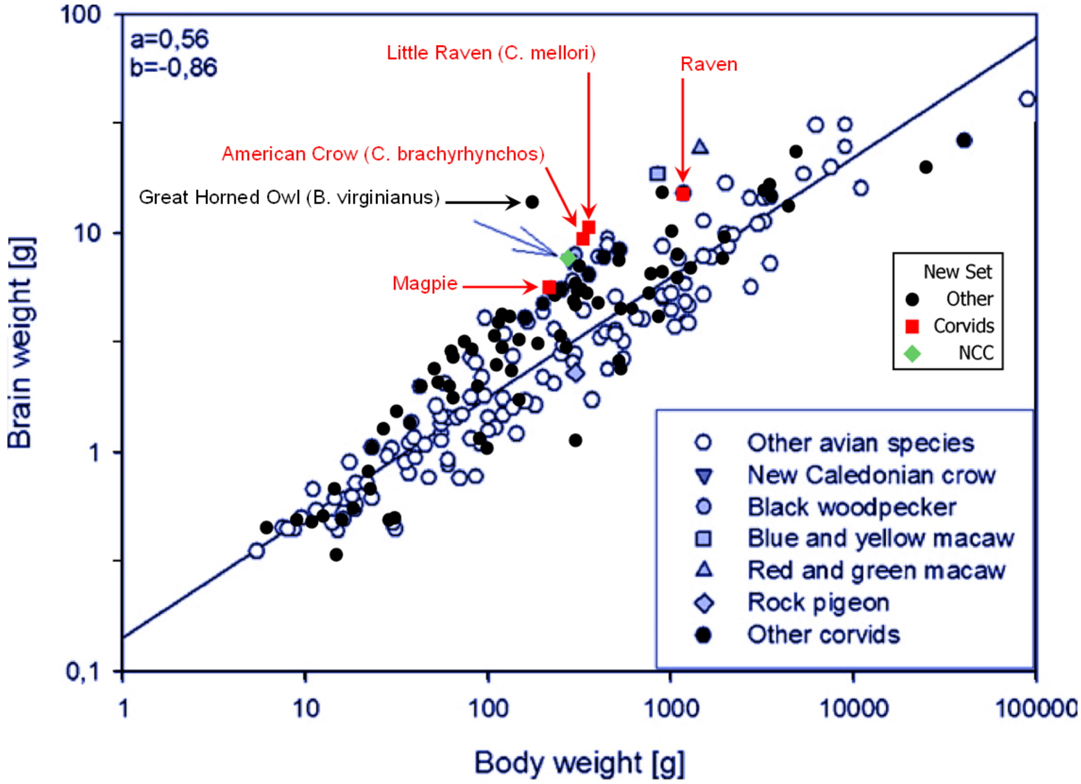

Figure 5-1. Plotting log brain mass against log body mass data from two datasets. Data from Cnotka et al. (2008), Figure 4, are represented in the lower-righthand key. Data from Iwaniuk & Nelson (2002) are overlaid, represented by the middle-right-hand key. The near identical values attained for the common raven and magpie suggest the datasets are comparable, and the two additional species (the little raven and American crow), demonstrate a relatively larger brain mass/body mass index than the NC crow.

A second NC crow neuroanatomy study set out to determine which brain structures –and by proxy, which cognitive abilities – demonstrate the greatest encephalisation when compared to other passerines (Mehlhorn et al., 2010). Four areas correlated with associative and motor-related skills – the mesopallium, striatopallidal complex, septum and tegmentum – were found to be enlarged in comparison to sparrows *Passer domesticus*, European jays *Garrulus glandarius*, and carrion crows. However, the statistical methods used to draw these conclusions may not be suitable. The authors generate their data by calculating the distances between observed brain mass values and expected allometric values based on their body mass (i.e. they plot a regression slope of log brain mass against log body mass for all species, and then calculate the distance between observed values to the regression slope (the residuals)). Ideally the analysis should use a single model to identify sections of brain that are significantly larger or smaller than average across all species (Crawley, 2007). Instead, they use multiple t-tests with two comparisons for each brain region, first comparing NC crows to pooled data for all other passerines (violating assumptions of independence), and then NC crows with carrion crows. The authors account for repeated tests by using a Bonferroni correction, reducing the alpha to 0.025, but this fails to account for the 17 repeated tests for each brain region, and overall we should expect 0.85 out of the 34 tests to appear significant by chance alone. However, reducing the alpha to 0.0015 would probably be overly conservative (Perneger, 1998). Irrespective of this oversight, the pooled passerine and carrion crow comparisons failed to compare NC crows directly with European jays, whose relative brain size is larger than that of NC crows according to their own data (jay: 26.7mm^3/g; NC crow: 26.3mm^3/g). Retrieving data from figure 2 of Mehlhorn et al.'s paper I have analysed the data using an ANOVA with a post-hoc Tukey test to investigate the pairwise comparisons between each species' mesopallium mass (see section 6.2.3, where I use the same statistical methods to compare maximum binocular overlap between *Corvus* species). Comparing log mesopallium mass / log body mass between species reveals no significant difference between NC crows and European jays (Tukey P=0.99), or carrion crows (Tukey P=0.45). However, the authors calculated their response variable in a different way, comparing observed mesopallium weight with the expected residuals of each species calculated from a single regression plotted through all species. Using a single regression for all species to compare specific data subsets could be erroneous because: (i) the slope is highly influenced by the species selected (and see criticism of Cnotka et al., 2008, above), and, (ii) because the slopes of each species could exhibit different relationships, which must be verified using a common slope test (Warton et al., 2006). When the data are scrutinised we find that the intraspecific regressions for all species except the carrion crow are negative, with lighter individuals having heavier mesopallia (in absolute terms). Thus there is no evidence to suggest all species exhibit the same scaling characteristics of body mass with mesopallium weight. Nevertheless, when I repeated the ANOVA using this allometric response variable based on the distance of each data point from a single regression through all species (equivalent to an F-test, Warton et al., 2006) I found little evidence for a significant difference between NC crow and European jay mesopallium indices (Tukey P=0.10 using the regression in figure 2 from Mehlhorn et al. (2010), P=0.07 from my own regression, a t-test is also not significant P=0.12). The differences between my own regression and that shown in Mehlhorn et al.'s paper are likely to result from the disparity in their reported sample sizes for sparrows (n=4) and the number of points shown in their figure 2 (n=3).

In conclusion, there does not yet appear to be sufficient evidence to support the theory that NC crow brain anatomy is markedly different to that of their close relatives. This is an interesting finding in itself; some authors argue that tool-use evolved as a domain-specific cognitive adaptation (van Schaik et al., 1999), while other evidence suggests it is a domain-general ability possessed by intelligent non-tool-using animals (Bird & Emery, 2009a). The fact that there are no clear brain area enlargements (based on my reanalysis) in a species that depends so heavily on tool-use (Rutz et al., 2010) in comparison to their non-tool-using relatives supports the domain-general arguments. However, this anatomical evidence cannot rule out adaptive shifts of cognitive roles in specific brain areas; for example, the precursors of tool-use behaviour in juvenile NC crows have recently been linked to the ontogeny of caching behaviour in common ravens (Kenward et al., 2011), see chapter 12. The European jays' caching behaviour is likely to be monophyletic with *Corvus* caching behaviour (de Kort & Clayton, 2006), so perhaps the brain regions associated with this behaviour have shifted their roles towards tool-use without manifesting as a change in size, perhaps due to the constraints on weight imposed by flying.

6 CHAPTER SIX – MAPPING VISUAL FIELDS

6.1 Introduction

Vision is an essential sensory input for many animals, whether searching for food, scanning for predators or selecting a mate. Eyes positioned on either side of the skull – exemplified by ducks and rabbits – can provide panoramic coverage of the world, ideal for detecting potential threats from all angles. Primate and felid eyes represent the opposite extreme; with both eyes pointing directly forwards they can perceive depth accurately, peer through foliage with greater visual redundancy, and perhaps perform better in low-light situations (see section 5.1.2). Using the parallax between two eyes to judge depth (e.g. Foley, 1980) means the head can remain stationary, whereas judging depth using one eye requires head movements (e.g. motion parallax (Rogers & Graham, 1979) or flow fields (Lee & Kalmus, 1980)). The positioning of birds' eyes varies markedly between species, primarily in relation to their feeding ecology (Martin, 2007). However, estimating where a bird can "see" around its head based on the angles of its eyes alone can be misleading, for example the short-toed eagles' (*Circaetus gallicus*) optical system produces a binocular field overlap in the horizontal plane of 40°, manifesting as large black pupils with apparently wide visual fields. Upon examination using the ophthalmoscopic technique Martin & Katzir (1999) find that only half of the optical width is served with vision from the retina. The ophthalmoscopic technique allows us to build up a complete three-dimensional map of where a bird can see around its head, factoring in the limits of the retina and optical system, eye movements and blind spots. It has been used in excess of 30 years on 52 bird species across 16 orders, from different ecological and behavioural backgrounds, making the method ideal for the standardised testing of interspecific comparative hypotheses (Martin, 2007). Various aspects of avian visual fields have been found to correlate with feeding ecology or parental behaviour (Martin, 2007; Martin, 2009) and can help explain phenomena such as the high rates of bird collisions with man-made objects (Martin, 2011). The width and height of the binocular sector is of particular interest; this part of the visual field is created where the fields of both eyes overlap, generally around the bill. Research has highlighted the trade-off between binocular and panoramic vision – some species appear to retain a binocular region so that they can accurately guide movements at close quarters or inspect the contents of their bill (e.g. Martin, 1986a; Martin et al., 2005; Martin & Piersma, 2009), whereas species without these limitations can develop panoramic vision for predator vigilance (e.g. Martin, 1986b; Martin et al., 2007).

Primates can easily watch their hands as they manipulate tools, moving their head and eyes independently of the tool to suit their visual needs; in contrast an NC crow's tool is closely and inflexibly coupled with its visual system. This could limit a crows' ability to see around the tool tip, particularly in mechanically confined circumstances, such as probing into a narrow hole. Evidence I have presented from the larva-cam experiments (see chapter 4) suggests that NC crows are sensitive to feedback from the larvae while probing, bringing into question the role of visual guidance during tool-use. Anecdotal evidence from handling NC crows and filming them probing for food using tools from within a tube (Figure 6-1), reveals that their eyes are highly mobile, and while probing they appear to bring them both directly forward. In order to determine whether NC crow visual fields have evolved to accommodate tightly coupled tool guidance in confined circumstances I used the ophthalmoscopic technique to compare NC crows to their closest relatives, none of which use tools habitually in the wild.

Figure 6-1. A still frame taken from video footage of a captive NC crow ('Uek') in Leutstetten, Germany. The crow is probing for meal-worms in a cardboard tube as part of a pilot study while the camera (Sanyo HD2000) films from the opposite end. The crow's eyes are clearly oriented forward during all tool-use, giving the impression they have a clear view of the tool, but we cannot know for certain whether the retinae of the eyes serves their vision at this angle without using an ophthalmoscope.

6.2 Methods

6.2.1 *Visual field Mapping*

I used the ophthalmoscopic reflex technique to measure visual field parameters (monocular, binocular and cyclopean fields) and eye movement amplitudes in 18 alert subjects across six

Corvus species (Table 3). The procedure is non-invasive and follows guidelines established by the United Kingdom, Animals (Scientific Procedures) Act, 1986, and Animal Welfare Act, 2006.

To locate subjects suitable for experimentation, I conducted an extensive search, using both my personal contacts and information found on the internet. I considered all *Corvus* species, and my final sample (Table 3) reflects what could be achieved within the logistical constraints of the study. All experimental subjects were captive animals in the UK, Germany or Austria, with the exception of two ravens that were caught near the Konrad Lorenz field station in Grünau, Austria, as part of an ongoing field project. These two individuals were released back into the wild immediately after testing and marking. All other subjects were immediately returned to their home aviaries once measured.

Each bird was held securely in a foam rubber cradle using fabric hook-and-loop fastener straps that wrap upon themselves (Figure 6-2). The feet and legs were carefully tucked away beneath the bird, and the head was held in position with a bill holder at the centre of a visual perimeter. To ensure a comfortable fit for the birds, I made species-specific bill-holders, using calibrated dorsal and lateral photographs of the heads of specimens from the Natural History Museum in Tring, UK. Holders were made from aluminium and polycaprolactone (thermoplastic, brand name: ‘Polymorph’) that could be moulded around the tip of the bill in situ. A fully adjustable, padded head rest prevented the head from moving backwards, out of the holder. Each holder took account of the size and shape of the bill of the species, and was further adjusted to fit individual subjects. The bill was held closed during experiments. While subjects had to be restrained for 30–45 min, they could be released from the apparatus immediately if they had shown any signs of distress (this was not necessary in any of our subjects).

Figure 6-2. Photograph of the experimental apparatus used to measure visual fields in birds. The bird's body is restrained in a foam holder with its head secured by a bill holder custom-built to fit each species. The head is positioned so that the eyes lie at the centre of the sphere delineated by the rotating semi-circular arm. An ophthalmoscope is used to record the angle of limits of the bird's visual field, read off from the semi-circular arm. The arm is then rotated 10 degrees and the process is repeated.

The visual perimeter uses a conventional latitude and longitude system, with the equator aligned vertically at the angle between the eye and bill tip. The head is positioned such that the angle of the bill to the horizontal approximates that which the bird adopts spontaneously when held in the hand. For consistency, I made all visual field measurements, having received training in the technique from Prof. Graham Martin.

Subject's eyes were examined with an ophthalmoscope held against a perimeter arm, and longitudinal positions were recorded to ± 1°. I established that the eyes of all subjects were mobile and could move independently. I determined the limits of the visual field, and the amplitude of eye movements, using the following procedure. The maximum and minimum longitudinal limits of the retinal visual field were measured in each eye at 10° (± 1°) intervals of elevation (latitude). The limit of the visual field was determined by the projection of the limit of the retina, the ora serrata. This can be seen as a clear difference between the bright reflection from the retinal surface and the black of the ciliary folds. Because of eye movements, however, the visual projection of these limits is not fixed, so I recorded the maximum and minimum limits of the visual field at each elevation. These were defined by the positions that the retinal margins spontaneously adopted when the eyes were fully rotated ‘forwards’ (converged) and ‘backwards’ (diverged). To map these positions, repeated measures of the projection of the retinal margin at each elevation were made in quick succession, and the maximum and minimum values were recorded. The amplitude of eye movements at each elevation was taken as the difference between these maximum and minimum values. Eye movements are complex rotational movements, but this procedure enabled me to measure explicitly any consequent translational effects on the limits of the visual field at each elevation. At some elevations, eye movements made little discernable difference to the position of the field margins, while at other elevations, effects were more pronounced. Due to inevitable obstruction by the holding apparatus, which varied in size across species (see above), visual field parameters were measured down to different elevations in the lower part of the frontal field in different species. To the rear of the head, measurements were typically possible down to the horizontal plane.

I also measured the optic axis of each eye (the line along which the cornea and the lens refractive surfaces are centred) by recording the perimeter co-ordinates at which the 1st and 2nd Purkinje images (reflections from the cornea and from the lens anterior surface) of a point source of light held close to the line of sight were most closely aligned.

In order to calculate the true angles of visual field limits, rather than the angles observed from the perimeter arm of the apparatus, I had to account for the separation of each individual's eyes at the centre of the apparatus (320 mm from the perimeter arm). Angles measured from the perimeter arm were corrected from a hypothetical viewpoint to infinity from the nodal point of each eye. Nodal separation was calculated from the distance between the cornea of each eye (measured from standardised and scaled digital photographs of the head of each subject held in the apparatus), and the divergence of the optic axes. This makes the assumption that the fundus (posterior portion of the eye) is semi-circular and that the eyes meet in the sagittal plane of the skull. From these data I constructed a 3D topographical map of each species' visual fields, and assessed how field boundaries were affected by eye movements (see above). The maximum width of the frontal binocular field (i.e., maximum binocular overlap) was determined on the basis of mean values (see Table 3), to facilitate interspecifc comparisons and functional interpretations based on the species' respective foraging ecologies.

6.2.2 *Meta-analysis of visual field data*

I assembled maximum binocular overlap data from all previously published studies of avian visual fields from Graham Martin's database built up over the past 30 years, and by systematic key-word searches ('bird* AND visual field*', 'bird* AND visual-field', 'avian AND visual field*' and 'avian AND visual-field*') in the 'Web of Knowledge' (Thompson Reuters;

see Table 6).

6.2.3 Statistics

Statistical analyses were performed in R version 2.11.1 (R-Development-Core-Team, 2011). Maximum binocular overlap for each species was calculated as the mean of each individual's largest binocular overlap. Maximum binocular overlap was compared between *Corvus* species using analysis of variance (ANOVA), with a post-hoc Tukey test to identify whether differences between specific species are significant. Data were checked for normality of error using standardised residuals plots (Crawley, 2007), and no transformation was necessary. The Tukey test mitigates the phylogenetic non-independence of *Corvus* species by estimating the degree of difference between all pairs of species while simultaneously controlling for model replication. The Welch t-test for unequal variance was used to compare intraspecific with interspecific maximum binocular overlap between NC crows and passerines, and NC crows and non-passerines (Ruxton, 2006). Confidence intervals were set at 95%, all tests were two-tailed and the level of alpha (significance) was 5%. The parametric statistical methods used here do not account for the non-independence of species due to phylogenetic relatedness (Felsenstein, 1985). The fact that the NC crow's binocular overlap lies well outside of the range of all other taxa (see results section 6.3) suggests that phylogenetically controlled statistics would not reach a different conclusion. The statistics used here can rule out the possibility that NC crows have a binocular field width similar to that of any other species, but it does not explicitly test an evolutionary hypothesis. Therefore, in order to shed light on the evolutionary significance of the NC crows' binocular overlap I analyse their evolutionary rate of binocular overlap change in section 6.4.

6.3 Ophthalmoscopic Results

NC crows had a mean maximum binocular overlap of 61.5° ± 0.2 (s.e.m.), which is significantly greater than that observed in the five non-tool-using Corvus species measured in this study, and a previously reported value for the American crow *C. brachyrhynchos* (Fernandez-Juricic & O'Rourke, 2010) (GLM; model: MaximumBinocularOverlap = Species; $F_{6,12} = 19.311$; $P < 0.001$; all Tukey post-hoc tests are significant at $P \leq 0.014$; Figure 6-4, Table 3 and appendix Table 5). The average maximum binocular field width of NC crows exceeded that of other *Corvus* species over 140 degrees of elevation in the frontal field, spanning from the bill tip to behind the head (Figure 6-3). An exhaustive review of previously published material on avian visual fields yielded comparative data for 46 bird species across 16 orders (appendix Table 6). Using this material, I found that NC crows have a significantly larger maximum binocular overlap than all passerine and non-passerine species (Table 3 and Figure 6-4; Welch t-test for unequal variance: passerines (excluding *Corvus* spp.); n = 7 species; $t_{6.2}=9.16$, $P< 0.001$ (see appendix Table 7); non-passerines, on log-transformed data, n=38 species; $t_{38.5}=25.28$, $P< 0.001$ (see appendix Table 8)). While these analyses do not control for phylogenetic independence of data, the fact that the NC crows' maximum binocular overlap is so clearly outside of the distribution of all other bird species makes statistical tests somewhat redundant. NC crow binocular overlap is 10.5° greater than the next nearest species, the brown-headed cowbird *Molothrus ater*, and the NC crow is well above the 99% confidence interval of all groups (99% CI for *Corvus* spp. is 46.7°; passerines 50.7°; and all other birds 49.7°). Had the NC crows' binocular overlap been significantly higher than average, but within the distribution of other bird species these tests would prove more crucial. Although the NC crow has a larger eye movement amplitude than all other *Corvus* species in this study, this effect is not statistically significant, with the exception of the raven (GLM; $F_{5, 12} = 3.2$, $P= 0.045$; Tukey post-hoc test for NC crow and raven, $P=0.026$; for all other comparisons $P>0.05$). This is due to the high variation in eye movement amplitude measurements, possibly because judging the minimum eye movements (see section 6.2.1), is more difficult than the maximum.

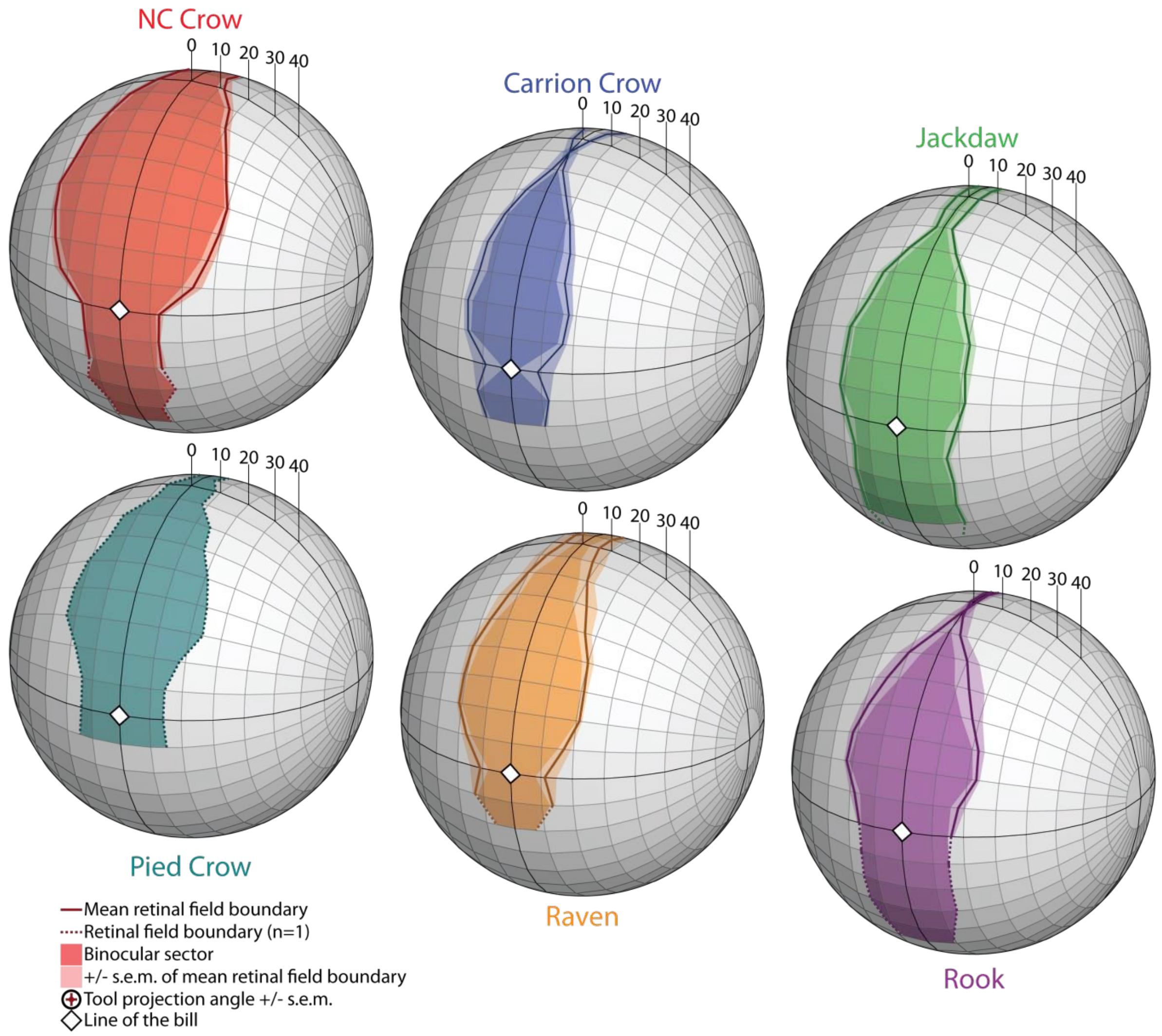

Figure 6-3. Orthographically viewed spheres with visual field projections overlaid. The diagrams use a conventional latitude and longitude coordinate system (with 10° intervals) with the equator aligned with the eye-bill tip angle. It should be imagined that the bird's head is positioned at the centre of the transparent sphere, with the bill tip and field boundaries projected onto the surface of the sphere.

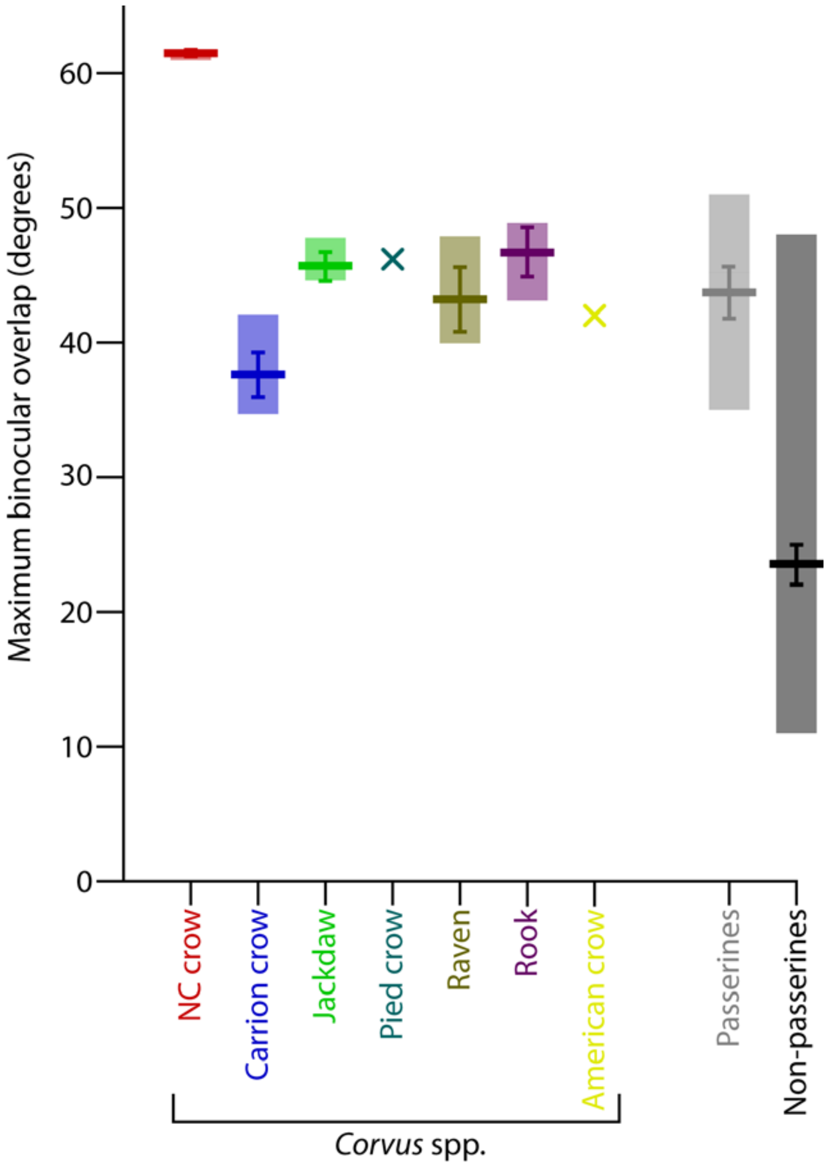

Figure 6-4. Maximum binocular overlap (in degrees) of three tool-using New Caledonian crows, six non-tool-using corvids (n= 5 carrion crows, 3 jackdaws, 1 pied crow, 3 ravens & 4 rooks), and other passerine and non-passerine species, showing mean maximum values (error bars show ±1 s.e.m. and shaded boxes show full data range, single data point shown for the pied crow, and mean value reported for the American crow (Fernandez-Juricic & O'Rourke, 2010)). While the degree of binocularity in non-tool-using corvids is similar to that of all other passerines measured to date, NC crows represent a highly significant outlier in this sample. Measurements for corvids were obtained as part of this study, and all other data were collated through an exhaustive literature review (see Table 3 and appendix Table 6). The maximum binocular overlap in the passerines group (excluding *Corvus*) is the brown-headed cowbird *Molothrus ater*, and the maximum in the non-passerine group is the tawny owl *Strix aluco*.

Species	N	Maximum binocular overlap		Maximum eye movement amplitude	
New Caledonian crow *C. moneduloides*[1]	3	61.5°	± 0.24	38.8°	± 1.64
Carrion crow *C. corone*[1]	5	37.6°	± 1.65	27.3°	± 3.53
Jackdaw *C. monedula*[1]	3	45.7°	± 1.03	26.5°	± 2.02
Pied crow *C. albus*[1]	1	46.2°		32.5°	
Raven *C. corax*[1]	3	43.2°	± 2.40	22.2°	± 2.74
Rook *C. frugilegus*[1]	3	46.7°	± 1.81	29.2°	± 1.86
American crow *C. brachyrhynchos*[2]	10	42°			
Passerines (excluding *Corvus* spp.)[2]	7	43.7°	± 1.92		
Non-passerines[2]	38	23.6°	± 1.48		

Table 3. Estimates of maximum binocular overlap (mean of maximum measurements ± s.e.m. in degrees), for tool-using New Caledonian crows, five non-tool-using corvids[1], and other species collected through an exhaustive literature review[2] (see appendix Table 6).

6.4 Phylogenetic Analysis: Methods & Results

6.4.1 Tree construction

In order to overcome the non-independence of phylogenetically related species, one must first establish each species' relation to every other species in a phylogenetic tree. In addition, most models require a fully dichotomous tree (i.e. no more than two branches from each node). Ideally, I would create my own tree based on sequence data from each species of interest. However, few of the species for which visual field data are available also have suitable DNA sequence data made available. I therefore constructed an amalgamated single tree from a number of published phylogenetic hypotheses that produced maximum likelihood trees from sequence data. My initial reference for tree construction was the peer-reviewed 'Tree of Life web project' (Maddison & Schulz, 2007), which produces a contemporary phylogenetic consensus based on published hypotheses.

The major avian groups were established as a result of an early explosive radiation, making the relationships between groups difficult to resolve and somewhat contentious. I constructed the overall bird hypothesis based on Hackett et al. (2008), which used ~32 kilobases of nuclear DNA from 19 loci, resulting in a fairly robust 'master tree'. This tree provided genus-level matches with a number of my target species, but further trees were required for resolving the following clades: The *Anas* genus phylogeny was based on Johnson & Sorenson (1999), the Procellariiformes from Penhallurick & Wink (2004), the Sphenisciformes from Baker et al. (2006), the *Apteryx* genus from Burbidge et al. (2003), the Corvidae from Ericson et al. (2005) and Feldman & Omland (2005), with additional Passeriformes from Barker et al. (2002), and further information on the location of black phoebes *Sayornis nigricans* from Ohlson et al. (2008). Trees based on different types of sequence data – such as mitochondrial DNA, or nuclear DNA from different loci – cannot simply be overlaid scaled to the same substitution rates because mutation rates at different loci are known to vary (Alberts et al., 2008). I therefore aligned trees to scale with the master tree from Hackett et al. (2008) ensuring that equivalent ancestral nodes scaled as closely as possible with equivalent branch tips to create a 'supertree'. I.e. I calculated the distance between equivalent branching points in Hackett et al.'s tree, and then scaled the other trees up or down so that overlapping branching structures match in length.

I was able to reconstruct a tree (Figure 6-5) resolving to the same genus or species in all but 7 of 52 species, and 3 of these could be placed within a sister genus. The relation between the blue duck *Hymenolaimus malacorhynchos* and pink-eared duck *Malacorhynchus membranaceus* remained unresolved, so the pink-eared duck was excluded based on a random coin-flip. The mourning dove *Zenaida macroura* was placed with its sister genus

Otidiphaps. The brown-headed cowbird *Molothrus ater* was placed with its sister genus *Icterus*. The Senegal parrot *Poicephalus senegalus* was placed with its sister genus *Psittacus*. I failed to find the squacco heron's (*Ardeola ralloides*) location within the Charadriiformes and it was not included. The location of the carrion crow *Corvus corone* has not been resolved, and was not included. Most importantly, the NC crow has not been resolved. There are a number of research groups currently working on the *Corvus* phylogeny, but in the interim I have positioned the NC crow in the most conservative position from the point of view of statistics looking at the rate of evolution of binocular overlap changes, i.e. as far as possible from all other individuals so that the branch lengths are as long as they could feasibly be, reducing the required evolutionary rate of change. Specifically, I placed NC crows near the root of *Corvus*, branching half way between the jackdaw's radiation from other *Corvus* and the last common ancestor of old-world jays (which also seems morphologically plausible). I gave it a branch length equal to the average *Corvus*. This places the NC crow as far from other Corvidae as possible, i.e. *Corvus* spp., the Eurasian magpie *Pica pica* and Western scrub jay *Aphelocoma californica*. Placing the NC crow any further within the *Corvus* clade would shorten its branch length quite considerably, at least doubling the required rate of evolution from the state of its last common *Corvus* ancestor from the position I have chosen.

6.4.2 *Phylogenetic Statistics*

A number of statistical tools have been devised to accommodate for the non-independence of species relatedness. The most commonly used is independent contrasts (Felsenstein, 1985; Garland et al., 1992; Purvis & Rambaut, 1995), primarily used for modelling a continuous response variable with continuous and/or categorical predictors. For example, using the 'pic' function in the APE package (version 2.7-1) in R (Paradis et al., 2004), one can use an independent contrasts analysis to investigate how maximum binocular overlap co-varies with a species' parental mode. The results support the observation (Martin, 2007) that narrow binocular overlap is generally found in species with precocial young ($F_{1,47}$=34.66, P<0.001). However, this approach is not suitable for analysing my NC crow data given they are the only habitual tool-using species to have their visual fields mapped. There is no standardised approach for mapping a single continuous trait across a phylogeny which might be subject to evolutionary pressures because most models assume the variables are neutrally evolving, whereas many continuous traits (such as body size) are obviously constrained by selective pressures (Hipp & Escudero, 2010). However, by comparing NC crows and other bird species to their last common ancestor I can estimate how quickly the NC crow might have evolved its larger-than-average binocular overlap. Using the 'ace' function in the APE package I reconstructed ancestral states on a phylogenetic tree. This uses a Brownian motion-based maximum likelihood estimator to reconstruct ancestral states from tree-tip values based on Schluter et al. (1997).

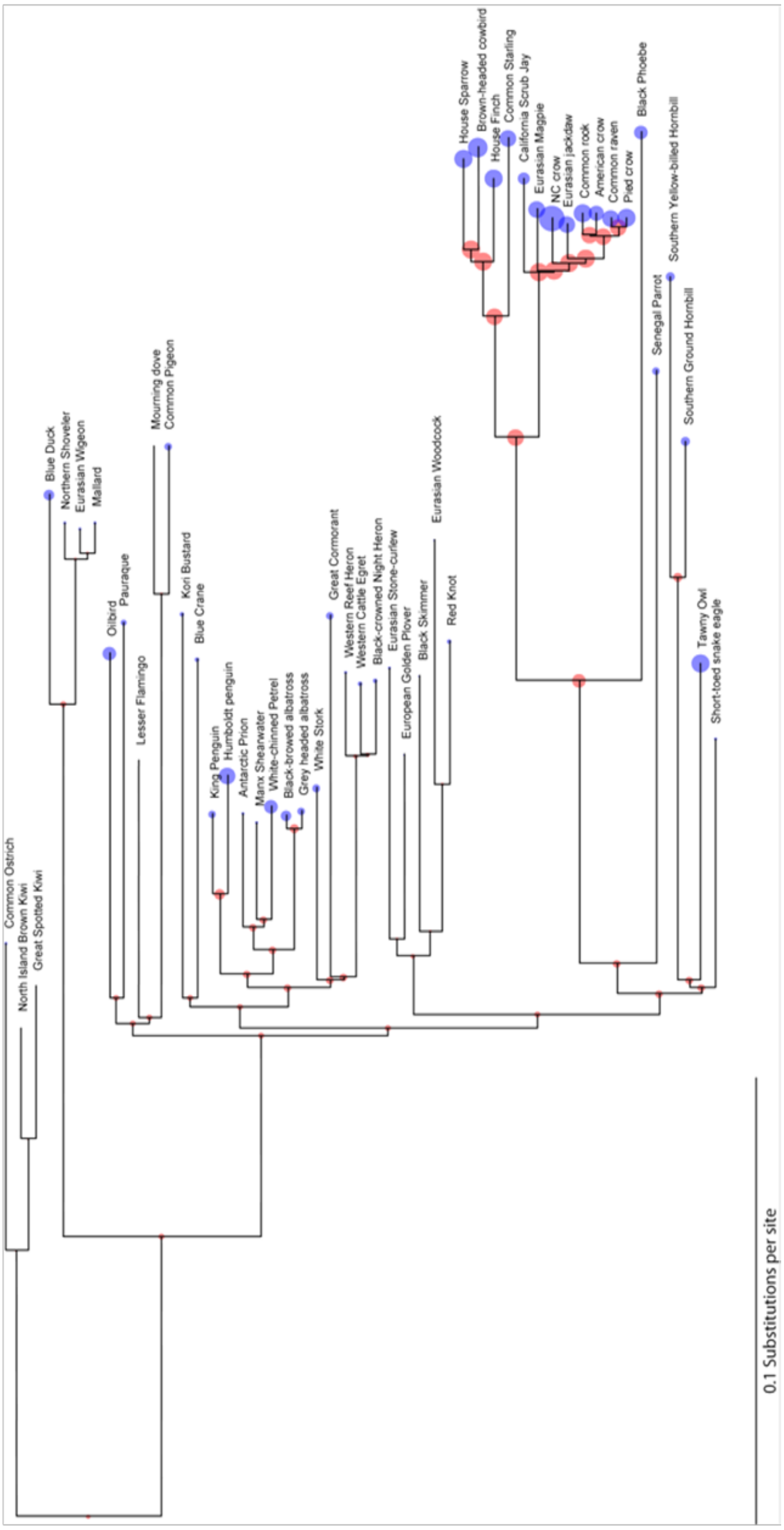

Figure 6-5. Tree constructed from a number of phylogenetic hypotheses revealing the relatedness of all species for which binocular overlap data were available. Blue circles at the branch tips are scaled to show the observed maximum binocular overlap values for each species recorded as part of this study and from the literature (see appendix Table 6). Red circles at the nodes within the tree are scaled to show the predicted ancestral binocular overlap values according to a maximum likelihood model. The scale bar shown is based on Hackett et al. (2008).

Next, I calculated the rate of change of binocular overlap in each species from the predicted binocular overlap of its nearest ancestor using the formula: (binocular overlap – binocular overlap of closest ancestor)/branch length. The results show that the NC crow has a rate of change of binocular overlap approximately twice as fast as any other bird species, furthermore, this rate is approximately ten times higher than the 99% confidence interval for the mean observed rate of all species (NC crow rate = 0.450, upper limit of 99%CI = 0.0450), see Figure 6-6 and Figure 6-7.

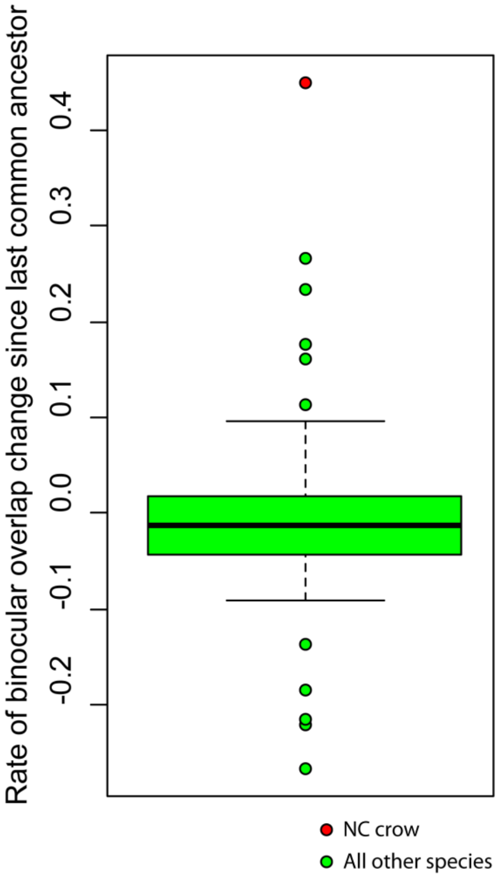

Figure 6-6. Box-plot showing the predicted rate at which each species' binocular overlap has changed since its last common ancestor. Central bar shows median, box and bars show the interquartile range, and circles show outliers. The NC crow (red symbol) demonstrates a rate of evolution nearly twice as fast as any other species (green symbols).

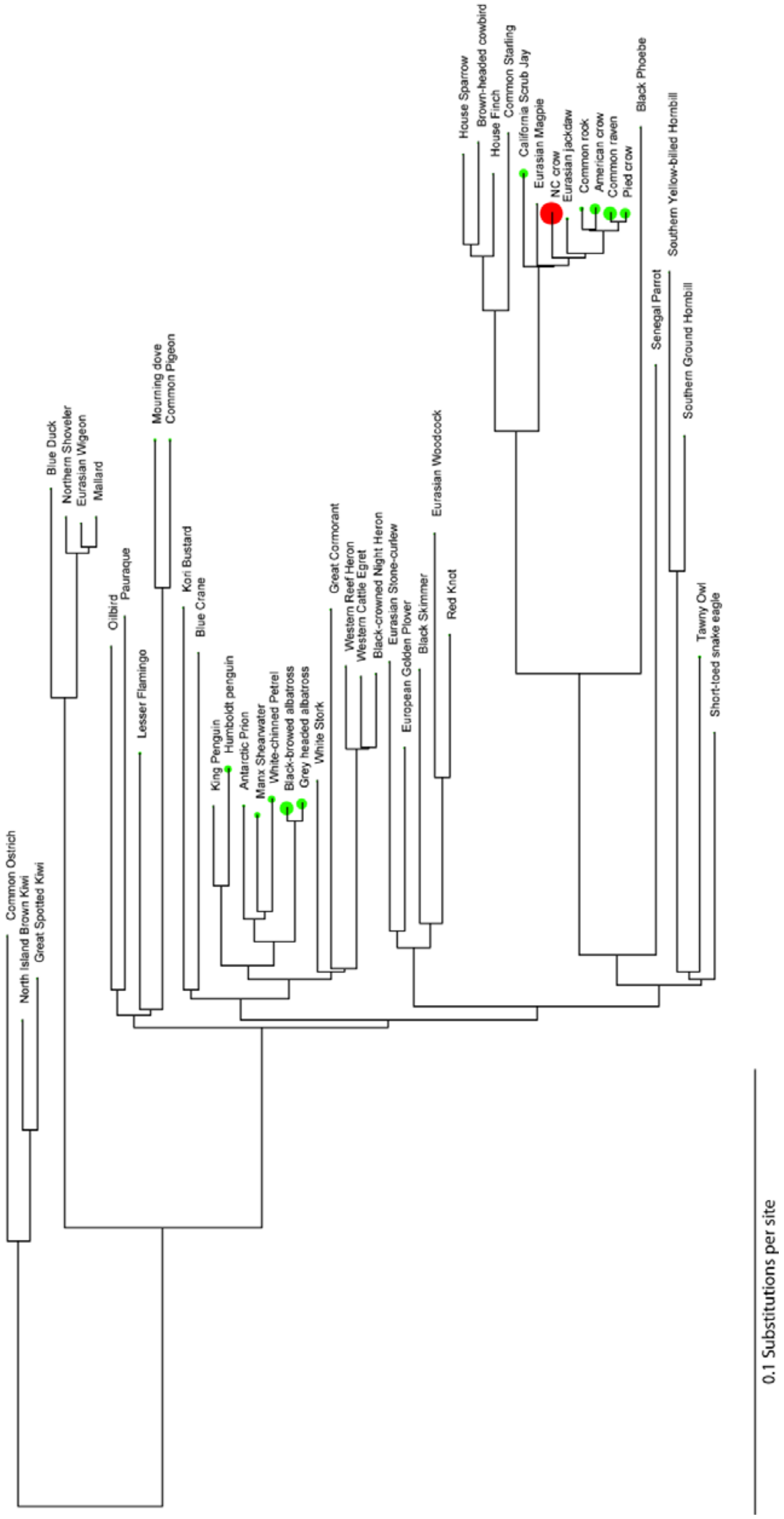

Figure 6-7. Phylogenetic tree. Circles at the tips are scaled to show the rate of change of binocular overlap of each species from its predicted ancestral condition. Note that this includes the rates of change for both an increase and decrease in predicted binocular overlap since the last common ancestor. The scale bar shown is based on Hackett et al. (2008).

6.5 Discussion

New Caledonian crows have a striking degree of binocular overlap when they bring both eyes forward, substantially greater than that of any other species measured to date. Does this unique morphological trait relate to their tool-use behaviour, and if so, how?

Phylogenetic analysis reveals NC crows' unusually large binocular overlap has evolved at a rate far higher than that observed in any other bird species for which data are available, suggesting their visual field topography has undergone strong selective pressures in recent evolutionary history. However, the methods I have used rely on at least two important assumptions that may not necessarily hold true: (i) that the phylogenetic tree is of a sufficiently high resolution in comparison to the typical evolutionary inertia of visual field topography. For example, if significant changes in visual field topography occur frequently throughout evolution then the binocular overlap of a species at the tip of a branch may have changed repeatedly since its common ancestor with another species in my dataset, making ancestral node reconstruction uninformative. The observation that the highest rates of binocular overlap occur on the shortest branch lengths suggests this may be the case. (ii) Reconstruction of ancestral states using Brownian motion estimates may not be valid for an evolutionary trait that is under evolutionary pressure, e.g. the blue duck has a much larger binocular overlap than other ducks in the analysis, resulting in a predicted ancestral node with intermediate binocular overlap, but this intermediate value might not be evolutionarily plausible if it sits half-way between discrete functional types of visual field topography (Martin, 2007; Martin et al., 2007). When a higher resolution phylogeny of Corvidae is published a far more rigorous analysis of the rates of binocular overlap change within the group will be possible. Nevertheless, my analysis confirms that the NC crow binocular overlap is unique in absolute terms, with reasonable evidence to suggest that it has also evolved under evolutionary pressure greater than that in any other species tested to date.

An ability to bring both eyes forward to create a large contralateral projection will offer NC crows greater visual redundancy in situations where small, close objects are likely to obstruct their vision in one eye, but not the other. Some have suggested that binocularity in primates evolved for this very function, allowing primates to see through the branches and leaves that clutter their vision at close quarters (Changizi & Shimojo, 2008). However, the substantial binocular region that this overlap creates could also theoretically be utilised for the perception of relative depth. While there is evidence that American kestrels *Falco sparverius* (Fox et al., 1977) and barn owls *Tyto alba* (Willigen et al., 1998) can use binocular vision for stereopsis, these species' eyes have fixed optical axes. There is currently no evidence to suggest that stereopsis can be achieved in species that have two eyes that can move independently (Martin, 2007; Martin, 2009); some species, such as kestrels, owls and ducks have eyes that are fixed, but many other species are able to make eye movements. These eye movements tend to saccade together, but can direct the two eyes in non-symmetrical ways (pers. obs.). Nevertheless, extractive foraging presents unique difficulties for monocular depth perception because of the constraints imposed while probing into a hole with a tool that is mechanically coupled to visual system. Motion parallax – for example – is unsuitable because it requires head movements perpendicular to the line-of-sight (Rogers & Graham, 1979). Direction of movement and time-to-contact could be calculated monocularly using optic flow-fields (Lee & Kalmus, 1980), but this could not allow estimations of tool-tip-to-target distance given the effective length of the tool changes with each grip adjustment and the tool tip does not move relative to the head. For example, a chicken could easily use flow-field information to peck at a grain on the floor, learning the length of its bill by association; but if its bill length were to change regularly – like an NC crow's tool – flow fields could no longer be used alone to judge time to contact the grain. Evidence I have presented from the larva-cam experiments (chapter 4) suggests that NC crows are able to judge tool-tip-to-target distance precisely, and that this ability is essential when attempting to extract live larvae that are vulnerable to being pierced and killed. I would therefore predict that if NC crows do not use stereopsis for depth cues they could use a combination of feedback mechanisms, for example, they could calibrate tool-tip-to-target distance using a combination of tactile feedback (i.e. probe the target using the tool and feel the resistance), together with subsequent depth feedback from proprioception and a number of monocular depth cues. These monocular cues might include: (i) optic flow; (ii) accommodation, which provides information on the relative distance of an object from the focal plane; (iii) perspective, for example, based on the tapering of the tool shaft; (iii) texture gradient of the tool and hole; (iv) lighting cues, such as shadows cast by the tool tip on a target.

Determining whether NC crows are able to use stereopsis would entail lengthy experiments training individuals to respond to random-dot stereograms; these are image patterns that appear random if viewed with a single eye, but can be combined through stereopsis into a meaningful stimulus. However, the use of stereopsis could be discounted more readily if I were to find that the NC crows do not use both eyes while using tools. Using behavioural experiments I set out to determine whether NC crows use both eyes while probing, and whether they change their probing strategies in response to visual feedback.

7 CHAPTER SEVEN – VISION FOR TOOL-USE

7.1 Introduction

New Caledonian crows have a larger frontal binocular overlap than any other bird measured (see chapter 6). Given the primary difference between NC crows and their *Corvus* relatives is their habitual tool-use behaviour it is reasonable to hypothesise that the two are linked. Additionally, evidence from the larva-cam experiment (chapter 4) suggests that NC crows are highly sensitive to feedback from larvae they are probing for, possibly dependent on visual information. Nevertheless, conclusive proof that NC crow tool-use relies on their unique vision requires behavioural experiments. I conducted experiments on wild-caught individuals, altering the visual properties of a probing task while monitoring the behaviour of their eyes.

The first goal of these experiments was simply to establish whether the eyes could be used for probing, i.e. assessing whether the retinae provide visual coverage of the tool under natural probing conditions through the use of an ophthalmoscope. Were the crows to maintain visual contact with only a single eye – using the other eye to keep watch for predators or conspecifics, for example – this would rule out stereoscopic depth perception (discussed in section 6.5). Secondly, I set out to determine how visual guidance affects probing behaviour by investigating whether the crows adjust the relative positioning of their eyes in response to changes in the visual constraints of a task. The way in which NC crows might alter their probing strategies as the hole they probe into becomes smaller would help determine whether they attempt to maintain binocular coverage of the tool tip, or whether a single (e.g. dominant) eye takes priority.

7.2 Methods

7.2.1 Apparatus

I filmed the eyes of unrestrained, naturally behaving NC crows during extractive foraging using a high-definition infrared ophthalmoscope. I built the ophthalmoscope from a Sanyo Xacti HD2 camera, recording at 30 fps (progressive), and a resolution of 1280x780 pixels. I removed the infrared-absorbing filter fitted to the camera's sensor, and replaced it with an infrared-transparent, visual spectrum-transparent filter which I made from acrylic sheet. A film of reflective/transparent (50%/50%) mirror was used to align an infrared light-source with the camera's view, thus converting the system into an ophthalmoscope. Birds are not thought to be able to see the >750 nm wavelength output of the infrared ophthalmoscope, or through the opaque filter used to alter the visual aperture of the hole opening, which had a 720 nm cut-off (Hart, 2001). I gave three wild-caught NC crows the opportunity to use tools to extract beef-heart pieces from a horizontal tube, with the ophthalmoscope filming from the distal end. Figure 7-1 shows the ophthalmoscope setup prior to installation in the aviary, and Figure 7-2A shows a still-frame sample of the footage.

The tube had a diameter of 35 mm, which was wide enough for both eyes to see the reward simultaneously, and is larger than most natural hole apertures (found to average 26.6mm, n=179, S.E.=1.3) (Bluff et al., 2010b), but small enough to prevent the entire head entering the tube. Subjects were supplied with straight, 21 cm-long bamboo sticks with a 3 mm diameter. Pieces of beef heart (ca. 1 cm^3) were presented at a depth of 20 cm from the tube opening, where they could not be reached by bill alone. I used three experimental treatments (shown in Figure 7-3c): (i) large aperture, the tube was left open so that both eyes could see the reward while probing (35 mm opening), (ii) small aperture, an opaque plate (made from transparent acrylic sheet covered with a film of infrared-transparent, visual opaque filter) was fitted over the opening of the tube with a 20 mm diameter hole, preventing both eyes from seeing the reward simultaneously, (iii) control, a transparent plate was fitted over the end of the tube with a 20 mm diameter hole to replicate the physical obstruction of the small aperture, with the visual properties of the large aperture. As all plates were transparent to infrared, the video ophthalmoscope could be used to film crow behaviour in all experimental conditions (even through the opaque plate).

Frame-by-frame video scoring was performed using Media Player Classic software (version 6.4.9.1), and using a macro script (autohotkey version 1.1.0) to import the time of events as they start and stop into Microsoft Excel 2007 (version 12.0.4518.1014). The timing of each grip change was recorded and the grips were categorised as left or right (i.e. the shaft of the tool projected out of the side of the bill to the left or right of the head), or centrally (i.e. the line of the tool continued into the bill and would not sit on the side of the head).

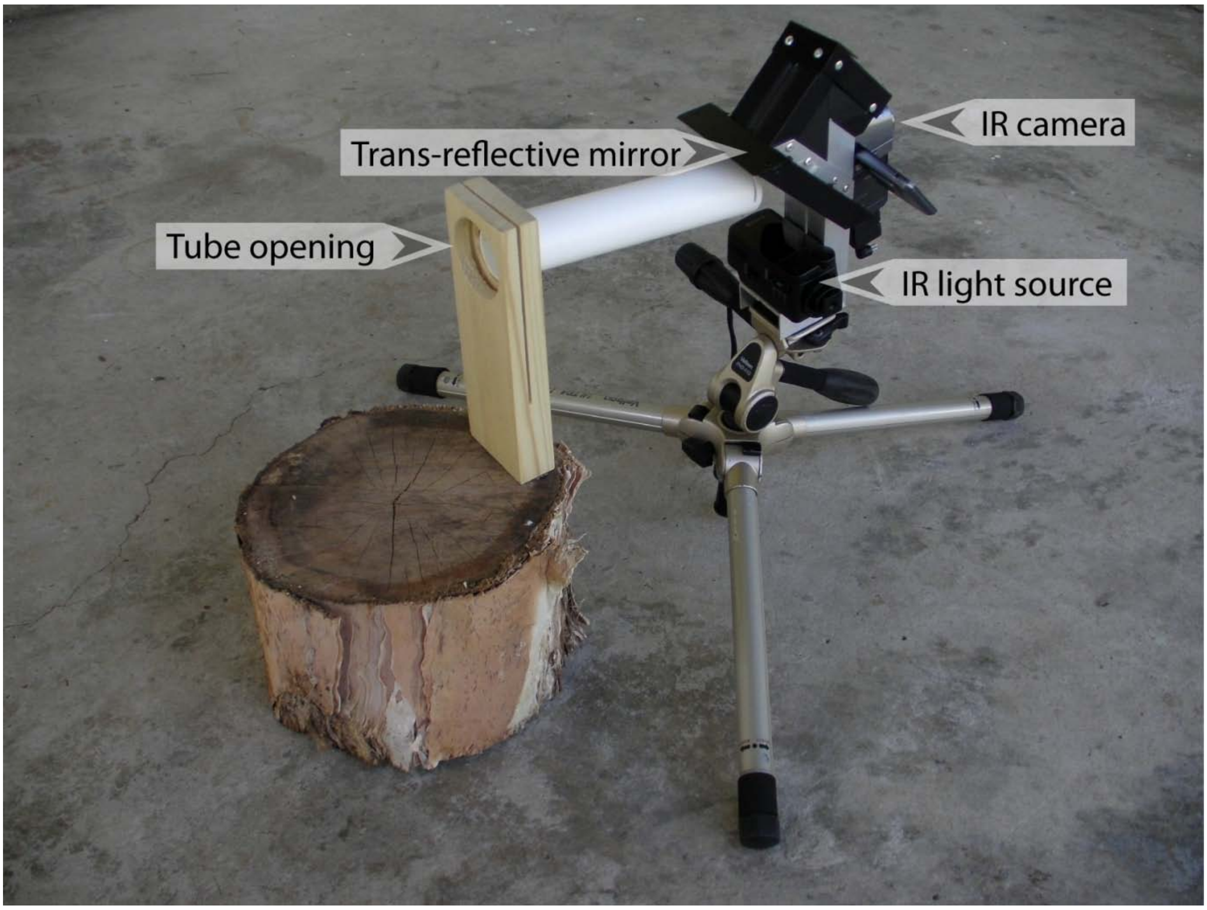

Figure 7-1. Photograph of the infrared ophthalmoscope setup prior to installation in the aviary. The apparatus was positioned so that the crows inside the aviary could access the tube opening (wooden sections on the left of the photo), but the ophthalmoscope and tube were left outside the aviary for easy access and trial setup.

7.2.2 Subjects

The crows were housed temporarily in an aviary measuring 3x3x2m, the first subject (A) was an individual female housed alone, and the two others (B,C) were a female and male of unknown relationship (Kenward et al., 2004), housed with a juvenile they were feeding (which did not participate in tool-use). The behaviour of B and C in relation to each other and the juvenile suggested they were mates. Gape colouration suggested all subjects were adults (see Rutz et al., 2007 SOM).

7.2.3 Statistics

Statistical analysis was performed in R version 2.11.1 (R-Development-Core-Team, 2011). Data were checked for normality of error using standardised residuals plots. Linear mixed modelling was conducted using the lme4 package (0.999375-35) in R, and a binomial error distribution was specified (angled or straight tool grip), using the Laplace approximation. Experimental subjects were included as random effects on the intercept, and trial number was included as a random effect on the slope (Crawley, 2007).

7.3 Results

I conducted a total of 118 trials across all subjects (crow A, n = 80; crow B, n = 10; crow C, n = 28, sample footage shown in Figure 7-2); all three conditions were presented in a random order within blocks of three where possible, however, as subjects B and C were housed together I attempted to allow both to interact with the apparatus before moving to the next condition, but sometimes one did not participate in trials in line with the other. Both eyes were consistently in a forward position whenever they were visible across all subjects and trials. Grip type was categorised into angled (tool projecting to the right or left of the bill), or straight (tool projecting straight into the bill). A total of 747 tool grips were recorded in the three subjects. I used a single GLMM to compare the relative frequencies of straight or angled (left or right) grips in the three experimental aperture conditions using the model: Grip = ApertureType + (trial|subject) where ‘Grip’ is a binomial response classing each new grip as angled or straight. When probing into the large aperture and control conditions subjects used proportionately more angled grips than straight grips when compared to the small aperture condition (large *vs.* small: z = -6.78, P < 0.001, control *vs.* small: z = -2.99, P = 0.003, see Figure 7-3b). Crows exhibited clear laterality, holding the tool to one side of the head >99.9% of the time; crows A and B gripped the tools on their right sides, while crow C gripped the tool on its left side, consistent with previously reported lateralised tool-use (Rutledge & Hunt, 2004; Weir et al., 2004). Average grip duration was 3.4 seconds (±0.13 s.e.m.).

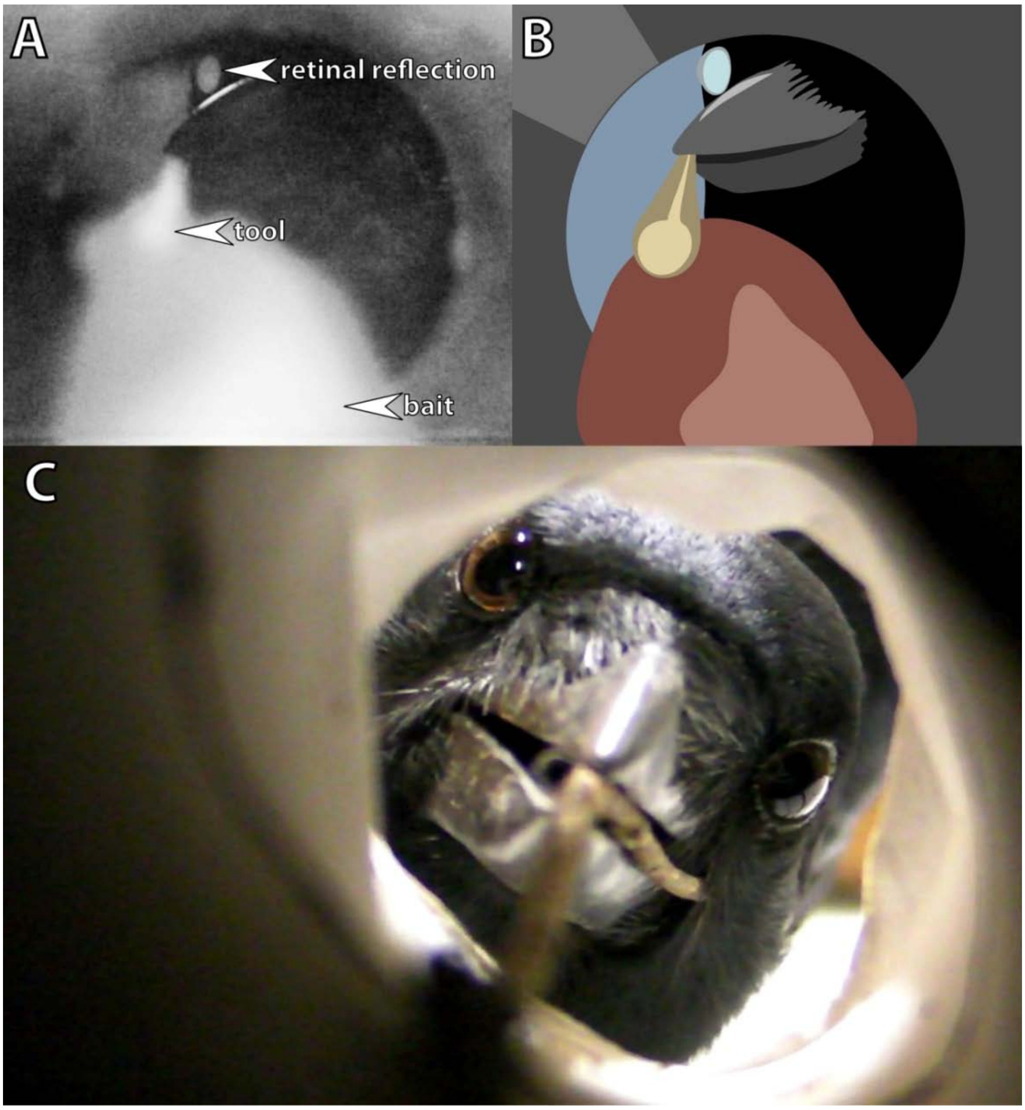

Figure 7-2. Single frame from an infrared ophthalmoscope video camera of a crow using an angled grip (a), and its schematic interpretation (b). The retinal reflection shows that the visual field of the contralateral eye embraces the tool-projection angle and that vision is not obstructed by the bill. (c) Still image of an NC crow probing into a tube during a pilot experiment using a straight grip (although the tool is bent), with both eyes clearly looking down the tool.

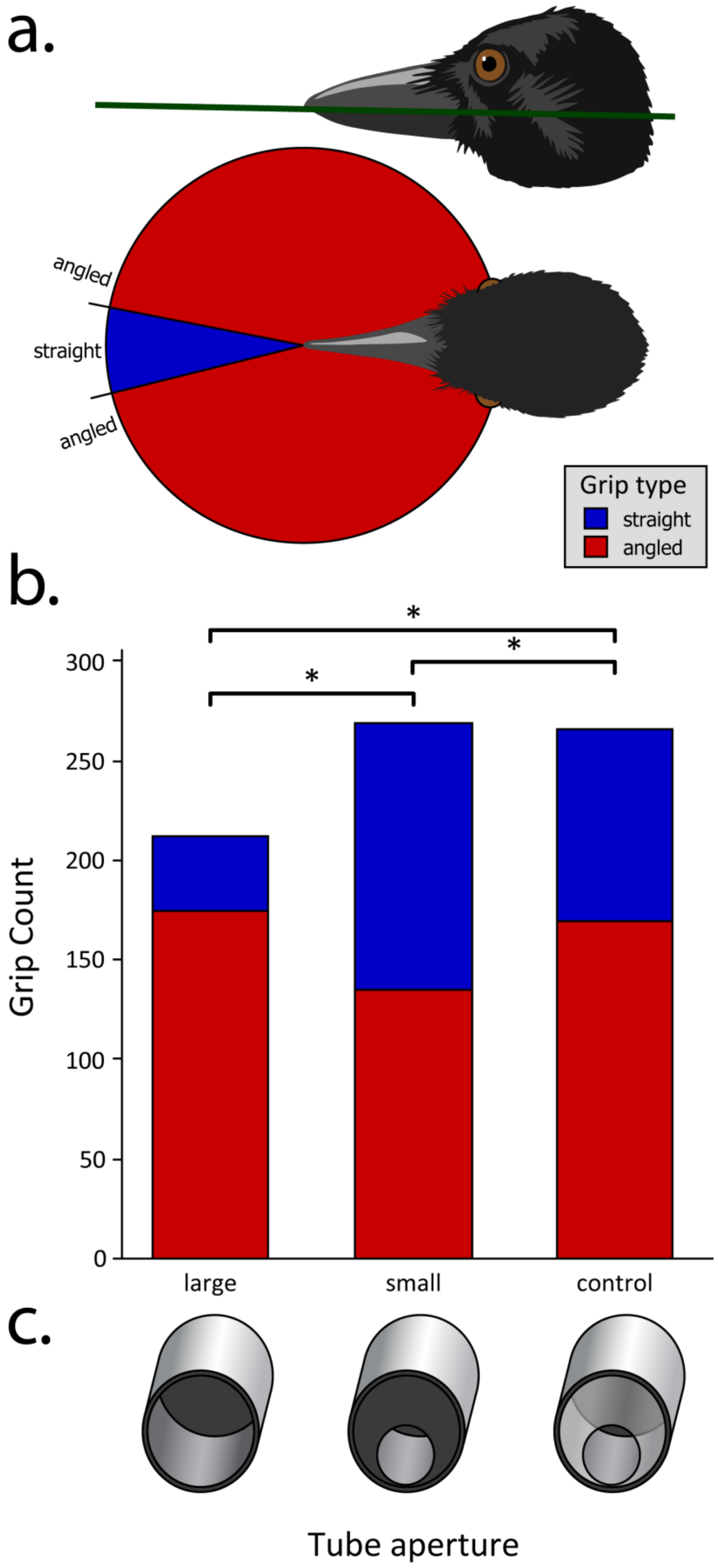

Figure 7-3. (a) Figure showing tool grip angles classified as angled (red) or straight (blue). (b) Graph showing the count for each grip type across the three treatment conditions with data pooled across all subjects. Proportionately more angled grips are used with the large aperture than the small or control conditions, although proportionately more angled grips are used in the control condition than the small aperture. (c) Diagrams of the tube aperture conditions.

7.4 Discussion

During tool-use NC crows bring both eyes forward, maximising the contralateral projections of each eyes' visual field. NC crows typically hold the tool in their bill tip, with the non-working end of the tool either held against their cheek (angled grip,) or inside the bill (straight grip (Rutledge & Hunt, 2004; Weir et al., 2004), see Figure 7-3A). When the aperture of a hole was large enough for both eyes to see into, the crows adopted an angled grip more frequently than a straight grip. In this configuration the NC crows' extensive binocular overlap enables them to look directly along the shaft of the tool with the eye contralateral to the tool projection (i.e., the eye on the same side as the cheek against which the tool is secured; Figure 7-2, Figure 8-1B), which is better positioned than the ipsilateral eye to maintain visual contact with the tool tip. Meanwhile, the tool-tip will lie closer to the central optical axis of the ipsilateral eye (i.e., further from the limits of the retina). When the aperture of the hole was reduced in size, so that only one eye could see into the tube, the crows used a straight grip more frequently than an angled grip (i.e., tool projecting straight forward, not resting against the cheek), which aligns the ipsilateral eye closer to the tool (see Figure 8-1B). In the control condition the visual aperture was large enough for both eyes to see into, but the physical opening was small; this controlled for the possibility that the mechanical properties of the opening could account for the observed effects on grip type. In these control trials, NC crows used an angled grip more frequently than a straight grip in comparison to the small aperture, mirroring the effect observed in trials with the large aperture. This shows that the visual properties of a hole opening alone are sufficient to determine the grip used by NC crows while probing. The results suggest that as visual hole apertures become smaller, a grip shift is induced to bring the ipsilateral eye closer to the tool, enabling it to maintain visual contact with the tip. Further tests could confirm the viewing priority of the ipsilateral eye by using even smaller tube apertures with a continuous measurement of tool-grip angle (rather than the binomial straight/angled used here). If the crows do adjust grip to maximise visual feedback from the ipsilateral eye I would predict that as aperture is decreased the tool would be aligned closer and closer to the ipsilateral eye until eventually the tool and eye are aligned on the opposite side of the head to that used for a large opening.

These findings are not consistent with maximising binocular coverage of the tool-tip, suggesting NC crows do not necessarily adjust their tool grip in order to assist stereoscopic vision. If the crows had aimed to maximise binocular tool-tip coverage I would have expected them to use an angled grip more frequently in small aperture holes, which would bring the ipsilateral eye closer to the shaft of the tool while maintaining visual coverage with the contralateral eye, effectively maximising the likelihood of maintaining binocular contact with the tool-tip. Instead, this experiment suggests that the dominance of a single eye influences probing strategy over binocular coverage. Nevertheless, we cannot rule out the possibility that both eyes are used for stereoscopic depth perception and further behavioural experiments using random dot stereograms similar to those used by Willigen et al. (1998) would be required to identify this ability.

Wild NC crows appear to demonstrate population-wide laterality dominance in tool-manufacture (Hunt, 2000a; Hunt et al., 2001), similar to the dominance of right-handedness in humans; but in captivity there is a clear 50/50 split between left-lateral and right-lateral tool-users (Rutledge & Hunt, 2004; Weir et al., 2004) similar to that of great apes (Byrne, 2004). Weir et al. (2004) suggested that tool-use and tool manufacture might therefore depend on different neural bases, but without further discussion of what these neural differences might be. This experiment implicates a low-level hypothesis for the disparity. Increased levels of laterality are associated with improved fine motor skills in great apes (McGrew & Marchant, 1999; Byrne et al., 2001; Braccini et al., 2010), thought to represent hemispheric specialisation for specific roles. In the case of motor skills laterality appears to develop randomly in NC crows and great apes independent of skill, and in humans laterality has no clear influence on any specific abilities (Hardyck & Petrinovich, 1977), suggesting motor control can specialise in either hemisphere. In contrast, vision demonstrates clear hemispheric laterality, apparently conserved across all vertebrates. The left hemisphere is typically specialised for foraging activities and prey capture, manifesting as right-directed movements, while responses to predators or novel stimuli are generally dealt with by the right hemisphere and the left side of the head (Rogers, 2002). This could help explain why NC crows tend to manufacture tools from the left edges of clockwise spiralling *Pandanus* spp. trees, but chose sides at random on anti-clockwise spiralling leaves (Hunt et al., 2001). The NC crows' left-hemisphere is likely to be responsible for locating suitable tool materials, and the left edges of clockwise spiralling trees are likely to be encountered more frequently by the crows' right eyes than the right edges. Subsequently, during tool-use in confined spaces where only one eye can provide feedback, laterality is dependent on the eye that has specialised on tool-control, possibly in a manner similar to the ontogeny of laterality in great apes with a 50/50 chance of developing in either hemisphere. This supports an observation of a wild NC crow which made tools from both the left and right sides of *Pandanus* spp.

leaves, but used the tool with consistent laterality (Hunt & Gray, 2004b). Thus the puzzling dichotomy of laterality in NC crows could result from low-level neural architecture conserved across all vertebrates rather than the human-like handedness proposed by Hunt et al. (2001).

8 CHAPTER EIGHT – BILL MORPHOLOGY

8.1 Introduction

Crow species are characterised by pronounced curved or hooked bills, thought to assist their varied and opportunistic feeding modes (see section 1.4.1; Goodwin, 1986). In stark contrast, New Caledonian crows sport a “peculiarly” straight bill (Kenward et al., 2004, p. 8). While this could be useful for holding a straight tool (Kenward et al., 2004; Rutledge & Hunt, 2004), the bill curvature ubiquitous in *Corvus* species is thought to be an adaptation for their ecological niche. The bill tip of all six *Corvus* species tested in my study fell at an elevation approximating to the centre, or just below the centre of their frontal binocular field (Figure 6-3). This visual field type is shared with other passerines (e.g. Martin, 1986a), and is thought to allow them to inspect and manipulate bill contents. Zweers & Gerritsen (1997) predict that a more pronounced bill curvature should enable a bird to visually inspect a larger volume of material in the bill than a straight bill of the same length, assuming the contents of the bill fall within the visual field. Kulemeyer et al. (2009) tested for this hypothesis in corvids, finding a positive correlation between probing frequency and bill curvature and length; rooks and common ravens – which probe in the ground and in carcasses respectively – exhibit more pronounced bill curvature than jackdaws and other corvids that rarely probe. However, this is only a correlative inference that does not necessarily underwrite a causal effect. In the wild NC crows readily adopt *Corvus*-like opportunistic feeding modes in parallel to their tool-using activities (Kenward et al., 2004). Furthermore, our isotopic signature analysis revealed that carrion accounted for a greater proportion of our crows’ protein intake than any other food source identified (see section 1.4.2; Rutz et al., 2010) – suggesting there are likely to be costs associated with a loss of generalist foraging adaptations. The NC crows' straight bill is likely to facilitate a tighter grip on a straight tool than a curved bill, and also allows them to rest the non-working end of the tool below the eye for lateral support (Kenward et al., 2004; Rutledge & Hunt, 2004). At present we can only speculate that the NC crows' bill may have become straight in response to their tool-use behaviour, as there is currently no concrete evidence to support this, or comparative hypothesis to test. My previous experiments have revealed that NC crows can see directly along a tool while probing (Figure 7-2; chapter 7), and that NC crows are likely to be highly dependent on visual feedback while probing (chapter 4). By combining visual field data with morphometric measurements I was able to assess whether any of the non-tool-using *Corvus* study species could, in principle, achieve levels of physical and visual tool control similar to that inferred for NC crows.

8.2 Methods

Tools can be securely held in the bill in only a limited number of ways (Figure 8-1B). In addition to the straight and angled grips described in the previous chapter, crows could hold stick tools perpendicular to the bill axis (grip 3 in Figure 8-1B), so that the working tip of the tool can be positioned in a region covered by the visual fields of the respective ipsilateral eyes. However, such a grip positions the line of the tool further from the eye than an angled, or straight grip (grips 1 & 2 in Figure 8-1B), making this grip less suitable for extractive foraging in a small hole (although a perpendicular grip is likely to be suitable for nest-building where the same physical constraints do not apply). For example, an angled grip allows visual feedback from a hole aperture approximately five times smaller than a perpendicular grip in Figure 8-1. Intermediate angles between perpendicular and angled grips (i.e. any angle between grips 1 and 3 Figure 8-1B) rely on the ipsilateral eye, and would therefore require an even larger aperture than a perpendicular grip. I modelled possible tool-projection angles that achieved simultaneously: (i) a stable tool grip; and (ii) the most direct view along the tool shaft.

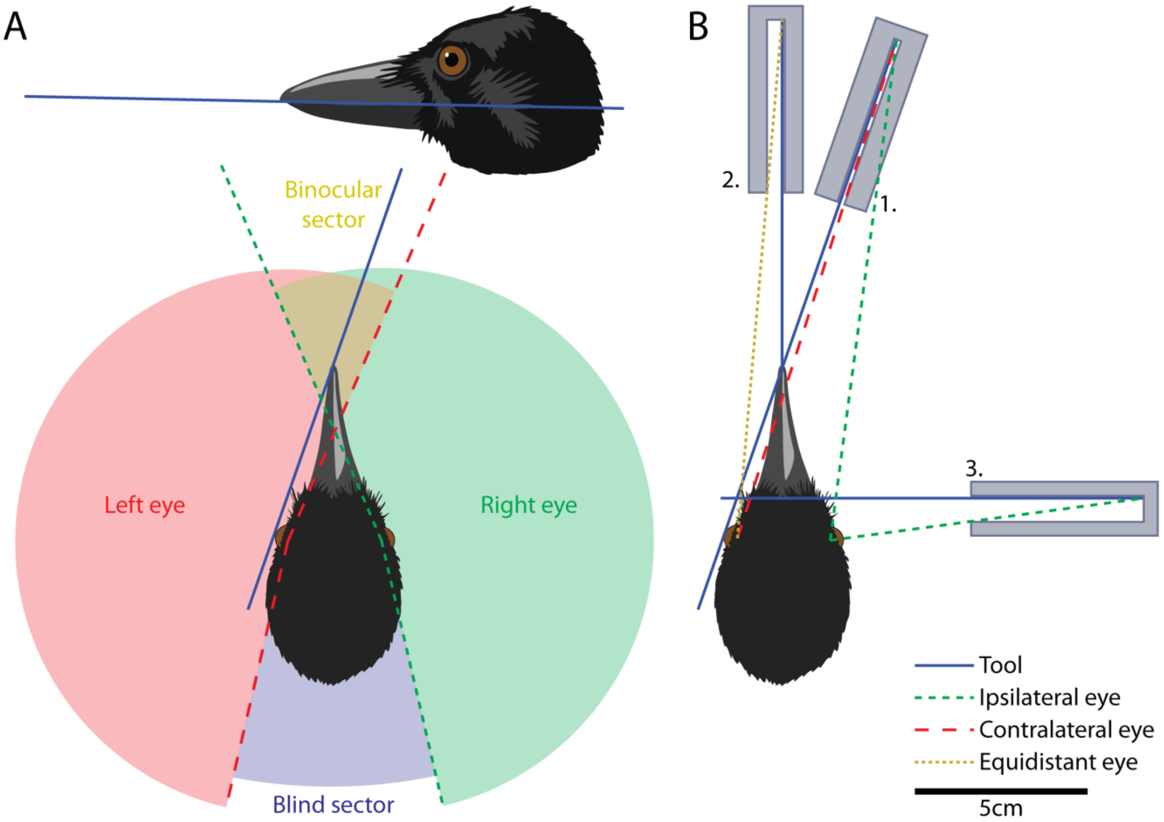

Figure 8-1. The geometry of tool-holding in NC crows. (A) Shows a typical 'angled' grip, which brings the tool into the NC crow's binocular sector where both eyes can see its working tip. (B) Illustration of the main grip modes that crows could theoretically use for extractive tool-use. Holding the tool perpendicular to the bill (B3) brings the tool tip into the field of the ipsilateral eye (green lines). The straight grip (B2) allows either or both eyes to look along the tool. An angled grip (B1) brings the tool into the field of the contralateral eye (red lines), allowing the contralateral eye to see into far smaller apertures than the ipsilateral eye.

8.2.1 *Measurement of hypothetical tool-projection angles*

I calculated the average sagittal tool-projection angle for each species from scaled macro-photographs taken of museum specimens and/or (where possible) directly from the experimental subjects of my visual field measurements (i.e., when the bill tip was not obscured by the bill holder). I independently showed three volunteer assistants – who were blind with regards to the hypotheses under investigation – a standardised and scaled photograph of each specimen on a computer screen in a randomised order, and without reference to species' identities. I asked them to locate the centre of the eye in each image and to position a circle, scaled to a 2-mm radius, where the tip of the mandible intersects the maxillary tomium (the cutting edge of the maxilla; see Figure 8-2 and Figure 8-2). Next, I asked them to draw a radius from the centre of the bill-tip circle and rotate it clockwise from the 6-o'clock position until it touched the lowest point of the tomium, then repeat anticlockwise with another radius.

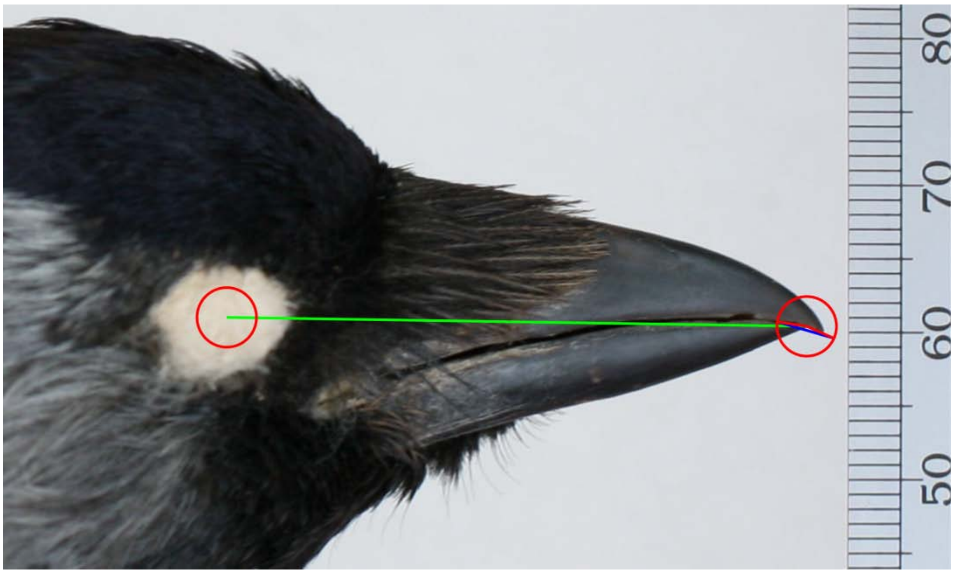

Figure 8-2. Example of the morphometric measurement of eye to bill tip angle, and tool projection angle from the bill. A circle is placed centrally over the point where the tip of the cutting edge of the mandible intersects the cutting edge of the maxilla (the tomium). Two radii are then drawn from the centre of this circle to the edge and rotated from a 6-O'clock position until the line touches the tomium.

The average angle of the two radii was used to estimate sagittal tool-projection angles if each individual were to hold a tool in their bill tip (angle α in Figure 8-2). Each experimental subject's mean coronal tool-projection angle was measured from the line between the bill tip and the outer edge of the centre of each eye relative to the mediolateral (left-right) axis. The overlap between the coronal tool-projection angle and the limit of the subject's visual field at the elevation closest to the mean sagittal tool-projection angle of its species was then calculated (β in Figure 8-2), in order to model each subject's ability to see parallel to the shaft of the tool.

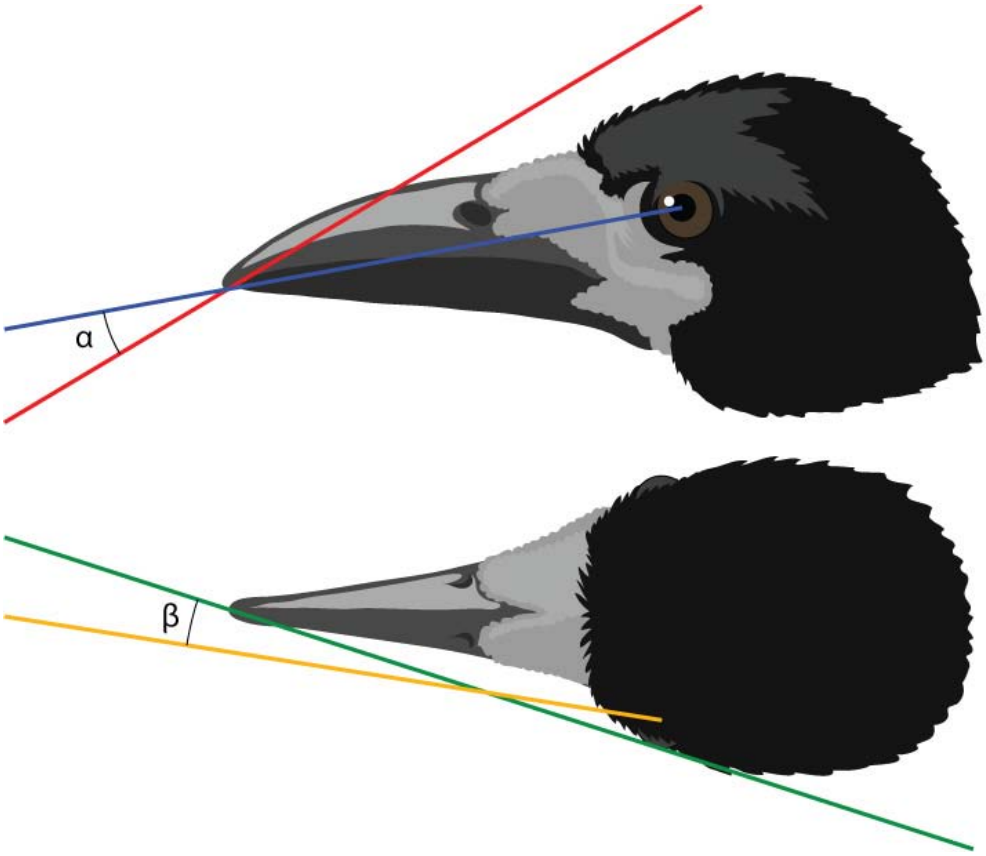

Figure 8-3. Modelling of hypothetical tool-projection angles, using the rook as an example. The sagittal tool projection (angle α) is calculated from the angle of the maxilla's lower ridge where it intersects the mandible (red) relative to a line from the bill tip to the eye (blue). The coronal tool projection (angle β) is calculated from the angle between the bill tip and a tangent to the outer edge of the eye (green) relative to the retinal field boundary at the elevation of the sagittal tool-projection angle (yellow).

8.3 Results

Non-tool-using crows have significantly lower elevation tool-projection angles than NC crows (museum specimen sample sizes: NC crow n = 3, carrion crow n = 5, jackdaw n = 3, raven n = 4, rook n = 3, experimental subject sample size: pied crow n = 1, rook n = 1 ; GLMM: formula: ProjectionAngle = source + scorer + species+ (1|source/scorer/species), where 'source' categories are museum or experimental subjects, ProjectionAngle is a continuous response variable with a Gaussian error distribution. NC crow projection angle is higher for all species comparisons at $P \leq 0.001$, specimen source made no difference at $P = 0.233$, and interobserver differences were not significant at P ≥ 0.586). This elevation is also observed to raise the non-working end of the tool above the eye where it cannot be secured against the cheek. Tools held by NC crows were modelled to project above the bill tip (i.e., from the crow’s perspective, the tool tip is at a higher elevation than the bill), and this estimate matches observations of natural tool projection angles reported in the literature (Rutledge & Hunt, 2004; Weir et al., 2004), and that observed in chapter 7 (see Figure 7-2).In contrast, tools held by all other investigated corvids would fall below the bill tip (Figure 8-3).

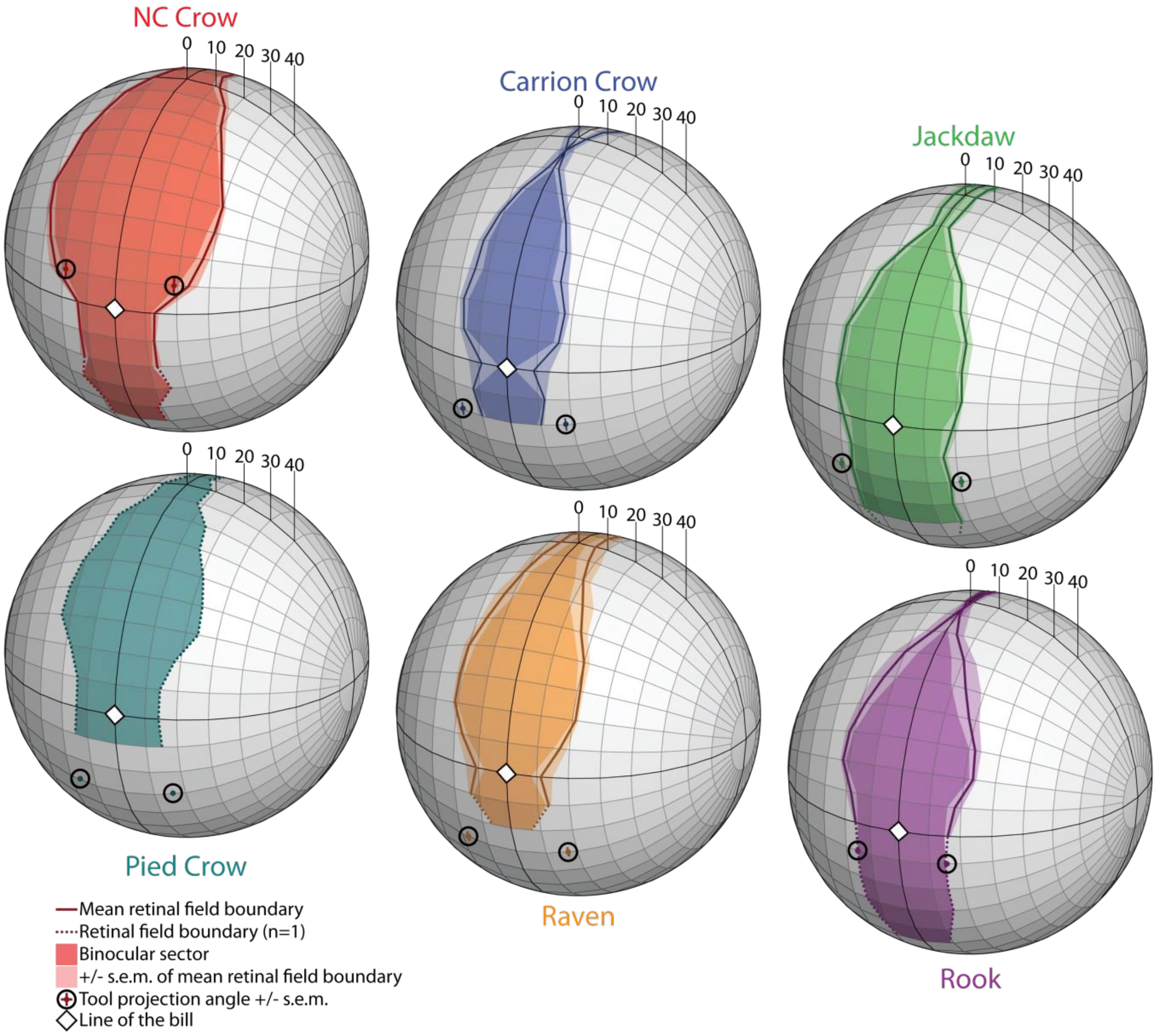

Figure 8-4. Orthographically viewed spheres with visual field projections overlaid (based on Figure 6-3). In addition, hypothetical tool-projection angles are plotted.

Species	N	Estimated overlap between visual field and tool projection	
New Caledonian crow *C. moneduloides*	3	3.9°	± 2.84
Carrion crow *C. corone*	5	-11.2°	± 4.47
Jackdaw *C. monedula*	3	-5.3°	± 0.28
Pied crow *C. albus*	1	-2.3°	
Raven *C. corax*	3	-5.8°	± 2.10
Rook *C. frugilegus*	3	-1.4°	± 0.17

Table 4. Estimates of the overlap between a hypothetical tool projection angle best suited to probing into a hole, and each species' visual field limits.

8.4 Morphology – Overall Discussion

The New Caledonian crows' unique combination of a straight bill and exceptional contralateral visual coverage enables them to look along a tool whist probing into a small hole to a degree unmatched by all other non-tool-using crows in my study. The curved bills of non-tool-using crows lowers the working tip of the tool into a narrower section of their binocular fields – which are already substantially smaller than the binocular fields of NC crows. This limits their ability to see the working tip if they were to insert it into a small hole, and would prevent them from resting the tool on their cheeks for lateral stability. These curved bills are thought to assist the visual inspection of the contents of an open bill in crow species probing in the ground or in carcasses (Zweers & Gerritsen, 1997; Kulemeyer et al., 2009), suggesting that the NC crow has forgone this ability in favour of a bill shape that is suited to gripping and visually guiding tools. An alternative interpretation is that the abnormally large contralateral projections in the NC crow visual field have evolved to mitigate the NC crows' reduced ability to inspect bill contents. However, behavioural evidence I have presented in the previous chapter shows that the visual properties of a task alone can induce a probing strategy change in NC crows, suggesting their tool-use is at least partially guided by vision, and that their large contralateral coverage is utilised during tool-use. Nevertheless, either hypothesis implicates morphological adaptation of the bill and/or visual field in response to tool-use.

Evidence I have presented from visual field mapping, behavioural and morphological lines of investigation provide strong evidence that NC crows possess morphological features that support tool-use behaviour, and to my knowledge these adaptations are unique among non-human animals. My findings cannot pinpoint the causal relationship between tool-use behaviour and morphology, specifically which came first; however, two further sources of information could shed light on this. First, comparative evidence from other extant bird species which are habitual tool-users could provide support for my findings. Unfortunately there is just one other habitual avian tool-user, the Galapagos woodpecker finch *Cactospiza pallida* (Tebbich et al., 2002). The remarkable variation in bill shape observed in Galapagos finches is thought to be indicative of their divergent selection pressures for different feeding niches (Darwin, 1845 p.380). In contrast, selection pressures in the corvids are likely to be convergent on a curved bill that suits their fairly uniform foraging mode (Goodwin, 1986). Therefore a comparative analysis of bill shape could not be conducted in the Galapagos finch in the same manner as the NC crow, whose straight bill is highly likely to have derived from a curved ancestral bill. Visual field data, however, could prove interesting, and I might expect the woodpecker finch to utilise larger contralateral projections than other Galapagos finches, similar to those aiding tool-use in the NC crow. Second, fossil evidence could confirm or refute my assumption that the ancestral NC crow had a curved bill. However, in contrast to tool-using hominids the likelihood of finding preserved fossil evidence that could date the emergence of tool-use independently of bill morphology is slim. The stone tools used by hominids have been well preserved amongst their bones, and the concurrent fossilised bones of their prey confirm the tools were used for hunting or butchering (e.g. Shipman & Rose, 1983). The small organic tools used by NC crows are unlikely to be fossilised, and evidence from fossil or sub-fossil NC crow remains (such as bill wear consistent with tool-use) is unlikely to be conclusive even if it were discovered. Therefore we cannot currently establish whether the ancestors of NC crows possessed morphological features that predisposed them to tool-manufacture and use, or whether tool-use behaviour was expressed first due to unusual ecological opportunities, before exerting selection pressures that gradually shaped the species' visual system and bill morphology.

Recent experiments demonstrate that captive rooks possess the cognitive capacity for sophisticated tool-use (see section 9.2.3; Bird & Emery, 2009a). These rooks were able to maintain visual guidance of their tools through clear plastic apparatus used in the study, circumventing the tool-use limitations imposed by their visual fields and bill morphology. Nevertheless, I found that the rook's ability to see along a tool was superior to that of other non-tool-using crows due to their less pronounced bill curvature (see Table 4), which could provide them with superior visual feedback of objects manipulated around the bill tip. While cognitive adaptations may be necessary for habitual natural tool-use, the tool-using rooks demonstrate that they are not sufficient for its expression in the wild. If the cognitive abilities of rooks are representative of those possessed by the NC crows' non-tool-using ancestor – which seems probable given the fact that corvids are widely regarded as one of the most intelligent groups of non-human animals (e.g. Emery & Clayton, 2004) – it is likely that morphological factors and ecological opportunities (rather than cognitive abilities) limited their expression of tool-use. In the next part of my thesis I explore the role of cognition in tool-use, attempting to determine whether tool-use depends on some specific or general cognitive abilities.

9 PART THREE – COGNITION

9.1 Introduction

While observing a non-human use tools it is all too easy to imagine that the thoughts going through its mind are similar to our own, but has this anthropocentrism led us to overestimate the levels of causal understanding demonstrated by tool-users? There is certainly a correlation between sophisticated tool-use and perceived general intelligence, with the most advanced cases of tool-use documented in primates, cetaceans and corvids; and evidence suggests tool-use occurs more frequently in birds with a larger brain relative to body size (Lefebvre et al., 2002). However, these correlations cannot tell us what cognitive abilities are sufficient for expressing tool-use; perhaps more intelligent animals are more likely to adopt tools due to increased displacement behaviour or exploratory play rather than any higher-level understanding of the causal principles, or perhaps tool-use relies on domain-specific cognition (see section 5.1.3). Evidently animals are capable of interacting with and modifying their environment in remarkably complex ways based on inherited behaviours that are often considered less flexible than advanced cognitive abilities. Birds' nests and spiders' webs are impressive examples of this, although spiders have been shown to integrate complex error correction during construction and birds can build upon prior experience during nest building (Hansell, 2000; Walsh et al., 2010). Both field and laboratory tool-based experiments continue to advance our understanding of the cognitive abilities of non-human animals. Not only is tool-use well suited to behavioural experimentation due to the accessibility of observations, it is also a fascinating behaviour in its own right.

Although my empirical contribution to NC crow research in this thesis is primarily to their behavioural ecology and morphology it is important to consider the role of cognition in the NC crows' unique tool-use behaviour. Cognition has been a major area of research in NC crow studies over the past few years, but the experiments performed and conclusions drawn are often highly controversial. Therefore in this part of my thesis I first present a critical review of the evidence for tool-related cognition, comparing humans, tool-using animals and non-tool-using animals in an attempt to discover the cognitive pre-requisites for tool-use. I then briefly present a novel experimental paradigm that improves upon previous attempts to demonstrate whether non-humans have an 'understanding' of physical causality, and data from a simple experiment that could warrant further investigation.

9.1.1 Defining Tool-use

New Caledonian crows are undoubtedly sophisticated tool-users, but in order to put their tool-use behaviour into context I must examine the nature of similar behaviours in other species; this entails defining tool-use, which is no easy task. Few would argue that termite-fishing or nut cracking in chimpanzees *Pan troglodytes*, or larva fishing in NC crows qualifies as tool-use. But is an archerfish (family: Toxotidae) using water as a tool by shooting droplets from below the surface to dislodge prey from the water's edge (Schlegel et al., 2006), and how can this be distinguished from orangutans *Pongo pygmaeus* transporting water in their cheeks to raise the level of a floating reward (Mendes et al., 2007)? Or when birds drop eggs and tortoises onto rocks in order to crack their shells (Cramp & Simmonds, 1979), are they using the ground in a different way to the anvils used by wild chimpanzees and capuchins (Boesch & Boesch, 1990; Fragaszy et al., 2004)? Do antlion larvae (family: Myrmeleontidae) use loose sand as a tool when they throw it at prey who fall into their pit, undermining the prey's footing so that they fall down to the antlion's jaws (Beck, 1980; Botz et al., 2003)?

An early definition of tool-use proposed by Jane Goodall was 'the use of an external object as a functional extension of mouth or beak, hand or claw, in the attainment of an immediate goal' (Goodall, 1970, p.195). Under this definition the antlions' sand, the archerfishes' water drops, a spiders' web and a birds' nest could all be considered tools even though these behaviours strike less of an anthropocentric chord, perhaps because they are likely to be genetically pre-determined, with minimal propensity for a flexible response to changes in context. Benjamin Beck (1980) reviewed numerous cases of tool-use spread across many phyla, providing a definition that has been used by ethologists for many years:

> 'Thus tool use is the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool'.(p.10)
>
> ''Borderline' (or 'proto') tools differ in that they are not held or carried, and are generally attached at the time of use. Under this definition, hammers are considered to be tools, whereas anvils, which can serve the same purpose, are borderline (unless carried at

> the time of use – as sea otters do).
>
> Tool manufacture is defined as: ‘any modification of an object by the user or a conspecific so that the object serves more effectively as a tool’ (pp. 11-12)

There have been many subsequent attempts to re-define tool-use, yet none have managed to secure a foothold in the literature (e.g. Chevalier-Skolnikoff, 1990; Lestel & Grundmann, 1999). Some argue (e.g. St Amant & Horton, 2008) that Beck’s all-encompassing definition falters when it comes to cases of tool-use that have recently been brought to light (e.g. dolphins using sponges (Krutzen et al., 2005) or gorillas using a stick to gauge water depth (Breuer et al., 2005)), while other authors argue that these semantic notions of tool-use lead us to overlook interesting and flexible feats of construction (e.g. Hansell & Ruxton, 2008). Evidence from tool-using humans and monkeys suggests that our brains re-shape our body ‘schema’ while using tools to take into account the physical extensions of our limbs, possibly justifying Jane Goodall’s mechanical definition of tool-use (Maravita & Iriki, 2004). Many researchers assert that tool-use requires special cognitive abilities because it involves causally relating two or more objects that are external to one’s own body (Piaget, 1954; Parker & Gibson, 1977; Tomasello & Call, 1997; Povinelli, 2000; Tebbich & Bshary, 2004). But this assertion firstly requires an accepted definition of tool-use, and secondly assumes that the defined form of tool-use places specific cognitive demands on the user. Instead, it would seem sensible to define tool-use based on cognition; Seed & Byrne (2010) use goal directedness to single out sophisticated tool-users – such as chimpanzees, capuchin monkeys and NC crows – by assessing these species’ context-specific flexibility of tool-use and selectivity or modification of tool materials. Similarly, we can form a simple definition of tool-use based on the user's physical understanding: e.g.: 'tool use requires the subject to understand the causal relationships between two or more objects external to its own body'. Without the aid of language an animal can only demonstrate this through manipulation of physical objects (tools). In addition, this definition brings into play the epistemological minefield of the term 'understanding'.

9.1.2 Understanding 'Understanding'

The nature of 'understanding' has been discussed by philosophers at great length (e.g. Searle, 1980), but the term remains poorly defined and there are no clear means of testing for understanding in humans, let alone other animals (Bluff et al., 2007). Philosophers necessarily define terms from a first-person perspective, providing definitions of understanding that are formulated verbally rather than mathematically, and are impossible to prove through behaviour alone (Penn & Povinelli, 2007). But even basing our definitions introspectively on conscious human thought may not be sound: Libet's experiment (Libet et al., 1983) proved that our brains decide to initiate voluntary movements well before we are aware of our own conscious decision to do so. Thus conscious decision making as we know it is far too slow to account for our actions in many instances (Blackmore, 2010), suggesting our understanding of at least some of our actions is based on retrospective analysis of our own behaviour, a notion supported by empirical evidence (e.g. Silva et al., 2005). This retrospective form of consciousness could even process information in a qualitatively different way to that used for the initial decision elsewhere in the brain. Pinker (1994) suggests language is an evolved 'module' unique to humans (although see Tomasello, 1995), so post-hoc verbal structuring of thoughts could lead us into thinking our mental reasoning follows similar logical rules, when it could in fact depend on other adaptively evolved cognitive modules which process abstract symbols and hierarchies in subtly different ways (perhaps more akin to the modules used by non-verbal animals). Forming a usable definition of understanding therefore depends upon major advances in reconciling studies of human consciousness with neurological decision-making – which is perhaps the most ambitious question science and philosophy could ever tackle. In the meantime I will adopt a working verbal definition of understanding that draws on sufficient prior knowledge; for example, a human understands the trap-tube task (introduced in section 9.2.1) if they can visually inspect the apparatus and explain to another person what actions they will take, providing an analysis of the physical principles and cues governing their decision. While such a definition cannot currently be used on any non-human, and there is little evidence that normal human activities rely on this level of foresight, it can generate testable behavioural hypotheses based on the way in which an animal solves a specific task. Experiments testing for a non-humans' understanding generally present puzzles suitably different from any others they have been reinforced with previously, so that the only similarities shared with previous experiences must be based on higher-level knowledge of physical principles, such as gravity and solidity (e.g. Visalberghi, 1997; Povinelli, 2000; Weir & Kacelnik, 2006). Slow attainment of proficiency over many trials (e.g. > 10) would suggest trial-and-error learning is being used, and further experiments would be required to determine what cues the animal was using. If, however, an animal solves a novel task immediately many would suggest that: (i) In tasks with a limited number of options the subject may be using a simple rule based on the outcome of the first trial (e.g. a win-stay, lose-shift strategy), which must be ruled out; (ii) the animal 'understands' the causal properties of the task, although this will always remain an issue of epistemological contention; or (iii) the animal is successfully generalising from a similar, previously reinforced cue (e.g. from a similar task). The distinction between the last two hypotheses is generally based on the implausibility of such a generalisation (Weir & Kacelnik, 2006; Bluff et al., 2007), but assessing the implausibility cut-off level has often been somewhat subjective (e.g. Clayton, 2007; Taylor et al., 2007; Taylor et al., 2009a). However, as my working definition of understanding suggests, the impressiveness of an animals' understanding hinges on the nature of the knowledge being used to solve the task, and there is little evidence that even human behaviour relies on much more than individually learnt knowledge and generalisation, in spite of what we might think we understand when asked (Overskeid, 2005). For example, few cyclists can explain the physical principles keeping them upright and knowledge of these principles would not help them to learn how to ride a bicycle. Indeed, when asked to draw the correct positions of pedals, chains and frames on a picture of a bicycle people make frequent and serious mistakes, failing to demonstrate a conceptual understanding of the easily perceived workings of the system (Lawson, 2006). Almost all humans have considerable experience in using their lungs to interact with other objects (e.g. blowing out birthday candles, cooling food etc..), but when asked to inflate a bin-bag with just one breath almost all will fail; sealing the bag opening around their lips knowing full well that their lung capacity is insufficient for the task (the solution is to hold the bag wide open and blow gently into it, creating air-currents around the exhaled breath, BBC 'Bang goes the theory' series 1, episode 2, 2010). Many simple tools that rely on less readily apparent physical principles than gravity and solidity were invented well before anyone knew what the physical laws governing their functioning were, e.g.: blow-guns were invented and refined by many pre-agricultural societies thousands of years before Boyle's law could explain how they worked, and gun barrels were rifled long before the laws of conservation of angular momentum could explain why the gyroscopic effect was beneficial to the bullet's trajectory. Therefore, at most we can only hope to learn what form of individually learnt knowledge an animal is using – the more abstract the generalisation, the more impressed we should be with their performance. While in the strict philosophical sense we can barely attribute understanding to our own conscious experience, let alone other beings, from an evolutionary point-of-view it is still interesting to see whether the difference between human and non-human levels of cognitive abstraction are quantitative, or qualitative (Chappell, 2006).

In the following sections I review what we know about the cognitive abilities of NC crows and other non-humans in the physical domain; discussing the evidence for human-like levels of abstraction and generalisation. By comparing the cognitive abilities of non-tool-using species and habitual tool-users we can hope to infer whether the evolution of tool-use required advances in cognitive ability, or whether certain taxa are already mentally equipped to use tools, but lack the ecological opportunity, motivation, and/or physical ability. Ultimately, this question alludes to the likely selection pressures that have made humans so unique, in respect of both our tool-oriented and cognitive abilities.

9.2 Physical Cognition

9.2.1 *The Trap-Tube Task*

Gravity and solidity are surely two of the most readily apparent and predictable physical laws, yet there is currently scant evidence to suggest any non-human can mentally simulate these laws and plan their actions accordingly. The trap-tube is simple task designed to test for this ability, attempting to show whether an animal understands which direction they must move a reward enclosed within a tube in order to avoid a pit-trap. The task has evolved considerably over the past 17 years as new arguments and findings come to light. Visalberghi & Limongelli (1994) invented the paradigm using a trap-central, food-offset layout. While one capuchin of four eventually learnt to solve the task after 120 trials the authors were cautious in attributing causal understanding given the individual very slowly pushed the reward while paying fastidious attention to its movements, and would often change direction and stop only when the reward was nearly pushed into the trap. A control condition was then presented to the successful capuchin where the tube was rotated 180°, rendering the trap non-functional. In this control the capuchin still avoided the inverted trap, leading the authors to conclude that a simple distance-based procedural rule was being used to solve the task, rather than causal understanding. Subsequent studies have tested additional species, and have attempted to rule out associative cues using varied controls and transfer tasks. However, these secondary tasks did not always rule out simple procedural rules, such as always pushing away from the trap (Limongelli et al., 1995; see Tomasello & Call, 1997). Povinelli (2000) attempted to remedy this flaw by repeating the experiment on chimpanzees with the additional inverted trap control, although the previous experience of individuals in this task could have influenced the findings (see Whiten, 2001; Mulcahy & Call, 2006). The use of the inverted control was then called into question by Silva et al. (2005), who found that humans avoided non-functional traps in over 90% of trials simply because there is almost no cost in doing so; even though subjects told the experimenter that they understood the trap to be non-functional. Evidently, predicting a null effect such as this control is a weak way to test a hypothesis in comparison to predicting a specific behavioural outcome.

Subsequent studies recognised the counter-intuitive need to push the reward away in order to retrieve it – something known to be difficult for chimpanzees and humans (Köhler, 1925; Guillaume & Meyerson, 1930; Seed et al., 2009). Tebbich & Bshary (2004) addressed this by using a modified version of the trap-tube task on tool-using woodpecker finches (*Cactospiza pallida*), allowing them to push the reward through the tube, or rake it towards them. One of six individuals mastered the task in 100 trials, but the authors liken the method used to Visalberghi & Limongelli's successful capuchin. Mulcahy & Call (2006) present the option of pulling or pushing in the trap-tube task to a number of great apes (two chimpanzees, two bonobos *Pan paniscus*, five orangutans, and one gorilla *Gorilla gorilla*). Two orangutans and one chimpanzee succeeded in learning the reward-central, trap-offset test condition in 24, 48 & 60 trials respectively. Perhaps oddly given the findings of Silva et al. (2005), they did not avoid the non-functional inverted trap in control trials, but reverted to chance. Unfortunately the design of Mulcahy & Call's (2006) task and control does not rule out the use of surface continuity as a cue. Perhaps, like the successful capuchin, they were paying attention to the proximity of the reward to a break in the surface. Mulcahy & Call's study (2006) suggests the tool-using requirement of this task presents a significant obstacle to the subjects. After all, they are required to causally relate three objects: the tool, the reward, and the trap; so perhaps eliminating the need for tool-use might allow the subject to demonstrate its understanding of the function of the trap more easily.

Seed et al. (2006) adapted the trap-tube task for non-tool-using rooks (*Corvus frugilegus*), with pre-inserted plunger tools and a second trap. The trap on one side of the reward is functional while the other is non-functional, either being blocked off at the top, or lacking a floor so that the food falls straight through (Figure 9-1). Rather than a standard pushing or raking tool the reward in these studies is enclosed between two disks attached to a stick so that pulling or pushing on the stick moves the reward in the desired direction. Seven of eight rooks mastered the test conditions. Transfer tasks were then used that reversed the required response (e.g. pulling the reward away from a stimulus that was previously associated with success, or towards one previously associated with failure) so that the subjects could not use a simple procedural rule to solve the task. One individual passed these complicated transfer tests, perhaps demonstrating a causal understanding of the various configurations of functional and non-functional traps. However, Seed et al. note that the successful individual could have solved the task by forming a rule based on the observable features of the task, such as surface continuity, as proposed by Tomasello & Call (1997) and Povinelli (2000). A similar experiment with rooks that required transfer from a single-trap task to a two-trap task found that all seven rooks failed the transfer (Tebbich et al., 2007). The authors found no evidence for a causal understanding given the subjects' failure to transfer knowledge between tasks, and another study from the same group found that rooks were unable to demonstrate an understanding of the physical connection between a disk and reward in a setup similar to the pre-inserted tools of the two-trap-task; instead they relied on more obvious cues provided by the stick, i.e. pull on the end with less stick protruding (Helme et al., 2006). Interestingly a number of parrots (three macaws *Ara chloroptera*, one cockatoo *Cacatua sulphurea*, and six keas *Nestor notabilis*) failed the trap-tube paradigm, the authors noting that a lack of inhibition appeared to prevent them from changing their choice, even though they could anticipate the loss of the reward (Liedtke et al., 2011).

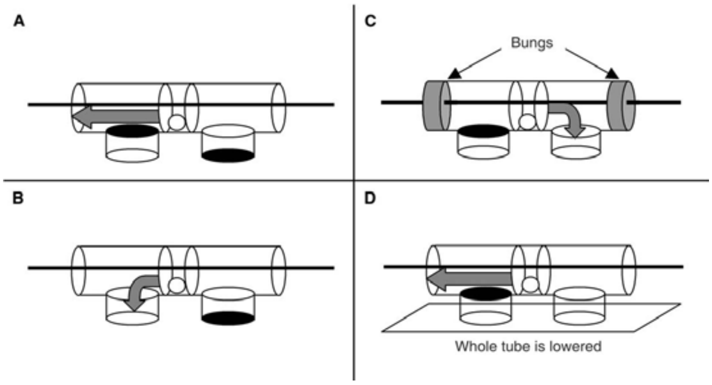

Figure 9-1. The trap-tube experimental setup used by Seed et al. (2006) (figure 2.). A & B are test conditions, and C & D are transfer tasks that reverse the causal properties related to visual cues such as the black blocking disk.

A recent study by Teschke & Tebbich (2011) compared the trap-tube performance of woodpecker finches (both tool-using and non-tool-using individuals), and the closely related non-tool-using small tree finch *Camarhynchus parvulus*. None of the small tree finches learnt the initial task, and no woodpecker finches transferred their knowledge successfully, failing to provide evidence that tool-use experience affects the woodpecker finches' levels of physical cognitive skills.

The performance of New Caledonian crows in the trap-tube paradigm is of particular interest given their assumed general intelligence (Emery & Clayton, 2004; Emery, 2006) and tool-use behaviour; perhaps their ability to use tools depends on a greater understanding of physical causality than the non-tool-using rooks tested previously. Taylor et al. (2009a) used a two-tube design and control tests similar to Seed et al. (2006) on NC crows, but with an additional trap-table transfer test (shown in Figure 9-2D), and without the same counterbalanced design. Three of six crows learnt to extract the reward reliably, and these subjects succeeded in passing some of the transfer tasks, including the trap-table.

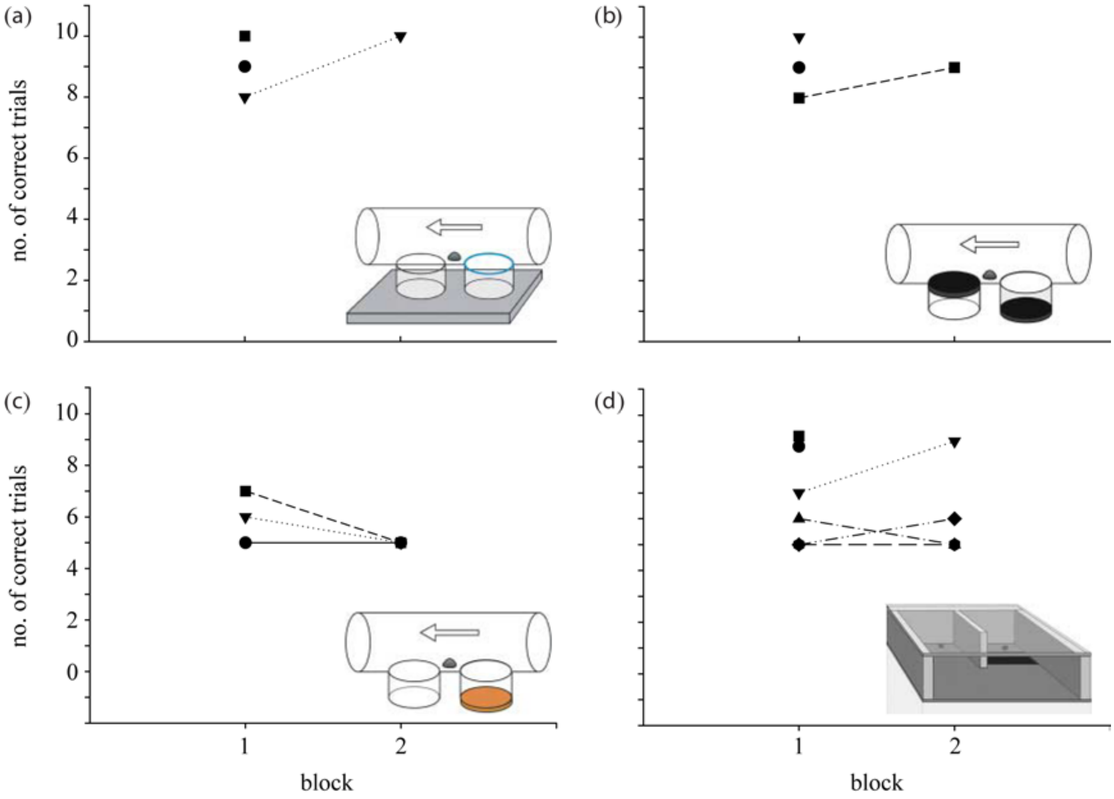

Figure 9-2. Reproduction of Figure 4 in Taylor et al. (2009), showing the results of the four transfer tasks offered to subjects that successfully solved the initial trap-tube task. Note the failure of all subjects in transfer task 3 (c), where they were unable to draw the reward over an open hole in order to retrieve it.

Taylor et al. concluded that their crows must have used causal reasoning; “Given the implausibility of the low-level explanations for the crows’ behaviour,” [i.e. individual learning and generalisation] “it appears that they solved the trap-tube and trap-table using the causal relationship surrounding object-hole interactions” (p.252). However, just because the crows were sensitive to causally relevant cues doesn’t necessarily implicate higher-level understanding. Transfer task 3 (Figure 9-2C) was the only task that required the crows to pull the reward into a hole, and this is the only task that they all clearly fail – demonstrating significantly higher latencies and frequent side-switching. Thus, the most parsimonious explanation is that the three successful crows were using surface continuity as a visual cue for trial-and-error learning that was also a causally relevant cue (e.g. Tebbich & Bshary's woodpecker finch (2004) was thought to solve the task based on surface continuity). Taylor et al. (2009a) argue that the trap-table and trap-tube are so visually different (square hole versus round hole, different colour surfaces, etc.) that the crows could not generalise associative cues across the tasks. But this is a highly subjective argument; particularly given the crows had previously been trained not to pull the reward into a surface discontinuity. When presented with similar results other authors have reached less dramatic conclusions (e.g. Tomasello & Call, 1997; Povinelli, 2000; Seed et al., 2006).

Adult humans should be expected to solve the trap-tube task and its secondary transfer tests within the first trial, or at least on the second attempt (Silva et al., 2005; Horner & Whiten, 2007). The clear failure of any non-human in 17 years of testing to solve the task in a comparable timeframe, and further failure to conclusively pass the secondary tests provides reasonably good evidence that non-human animals are finding solutions based on cues requiring less impressive feats of generalisation than those used by humans. While this is certainly good evidence for a quantitatively different level of abstraction, we cannot rule out a qualitatively different form of cognition in humans (Chappell, 2006; Bluff et al., 2007); for example, perhaps modern humans lead lives that expose them to the underlying principles of gravity and solidity with much greater efficacy than captive animals' initial trap-tube exposure. If this were the case then non-humans brought up in an environment intensely enriched with gravity-oriented tasks might learn to generalise from gravity-based cues better than other non-humans. It is also likely that humans have additional experience in *learning* to solve problems based on individually learnt principles. We still know very little about the cognitive techniques humans might be using to solve such causal tasks; if nothing else, the trap-tube should force us to think about physical understanding in humans and non-humans alike.

9.2.2 Connectedness

Connectedness has also been used to explore animal's causal understanding, for example, Povinelli (2000) tested chimpanzees' understanding of connectedness in an experiment where the subjects were presented with two strings, each attached to a banana with differing levels of connectedness or degree of contact. The conditions varied from fully connected with a knot, loosely connected with the banana resting on the string, high levels of contact with the string covering much of the banana (but not connected), to fully disjointed. Povinelli found that the chimpanzees tended to pull on the string with high contact, but no connectedness, rather than a straight string with a banana resting on top (though this is only a tenuous 'connection'). This led Povinelli to conclude that the subjects were not demonstrating an understanding of the difference between physical connection and degree of contact. Silva et al. (2008) recently replicated this experiment with humans, finding that they make the same errors when presented with the same task. The authors argue that the degree of contact is likely to be a very good predictor of connectedness in nature (following the laws of friction), and so little can be concluded from Povinelli's findings.

Pulling on a string in order to recover a reward is assumed to require an understanding of the means-end relationships between the physical objects (string, reward and subject's own body), and it has been documented in more than 10 bird species ((Thorpe, 1963), cited in Heinrich (1995)), and was noted nearly 500 years ago by Plinius (1554) (Seibt & Wickler, 2006). Heinrich (1995) found that one wild common raven (*Corvus corax*) could spontaneously pull on a string to retrieve the meat suspended below. The author originally assumed that this demonstrated insight on the part of the raven as there was no other explanation for its immediate solution to the problem that involves repeatedly pulling & holding the string. However, in this experiment the behaviour could be the result of quick learning and a direct attempt to manipulate the vicinity of the food, and additionally the individual's behavioural history with respect to string pulling was unknown. Seibt & Wickler (2006) demonstrate that a large proportion of individuals in a group of goldfinches (*Carduelis carduelis*) and siskins (*C. spinus*) could learn a string-pulling task on their own, and of those that could not a number could then succeed after being given the opportunity to learn socially. So it would appear sting-pulling can be learnt fairly readily by animals not known for their cognitive abilities, and that forms of social learning (such as stimulus enhancement or goal emulation) can influence the learning process.

When Heinrich & Bugnyar (2005) re-tested ravens with a string-pulling task (this time controlling for social learning and neophobia) they found that ravens proficient in normal string-pulling were also able to pull down on a string connected to a pulley in order to retrieve the reward, whereas ravens that were naïve to the string-pulling were not able to conduct this counterintuitive behaviour. The authors argued that this demonstrated an understanding of the means-end relationships in the proficient ravens, though there are other plausible explanations: firstly, the proficient group were heavily reinforced with string pulling from previous experience (irrespective of means-end understanding), so would be likely to pull on any string with more enthusiasm; and secondly, pulling a string down as opposed to up is not very different if the string is periodically restrained by the foot, in either case any action performed on the string in almost any direction (other than directly away from the foot) will draw the reward closer.

9.2.3 Selectivity

Flexible and adaptive problem solving can reveal an animals' intelligence (Emery & Clayton, 2004), and these attributes can be used to label animals as sophisticated tool-users (Seed & Byrne, 2010). But determining the adaptability of a behaviour can be difficult, as Hansell & Ruxton (2008) highlight with the fact that many innate construction behaviours (such as birds' nests and spiders' webs) can incorporate impressive capacities for flexible error correction. It is therefore difficult to determine whether the different tool dimensions used by wild chimpanzees for different foraging tasks (e.g. Boesch & Boesch, 1990) demonstrates a mental representation of the task's requirements (as postulated by Boesch & Boesch, 1993), or whether individual trial-and-error learning could account for the observed effect. We must therefore rely on controlled experiments that can assess an animals' flexibility under novel circumstances, eith in the laboratory, or in ontogenetic studies that can determine how tool use and tool-manufacture develop. Captive orangutans, gorillas and a Tonkean macaque (*Macaca tonkeana*) were able to select rake tools of a suitable length for a specific task (Ueno & Fujita, 1998; Mulcahy et al., 2005), and two capuchins were able to select tools of a suitable diameter (Anderson & Henneman, 1994). However, woodpecker finches did not spontaneously select tools of an appropriate length for food at an appropriate depth. Initially all woodpecker finches selected the short tools irrespective of reward depth, but over the course of the experiment three subjects learnt to select tools of a sufficient length (Tebbich & Bshary, 2004).

The ability in NC crows to spontaneously and flexibly select tools of an appropriate length was tested by Chappell & Kacelnik (2002); two subjects (Betty and Abel) were presented with ten tools of different lengths and a reward in a horizontal, transparent tube at different depths. Both crows spontaneously selected tools of an appropriate length more frequently than would be expected by chance, even when trials where crows selected the longest tool – which would otherwise be a suitable default strategy – were excluded (Bluff et al., 2007). Chappell & Kacelnik (2004) next tested the ability of these two crows to select tools of an appropriate diameter. Betty always demonstrated a strong prefference for the thinnest tool – which worked in all trial scenarios – even when she was forced to retrive it from a bundle at a small additional cost. This suggests her selectivity (perhaps due to ergonomic factors) outweighed her flexibility. However, when the two subjects were presented with raw tool materials (rather than pre-made tools), the diameter of the tools they manufactured incresed significantly with hole diameter. A follow-up analysis by Bluff et al. (2007) found that thicker tools were manufactured faster than thinner tools, suggesting the crows would only chose to manufacture the more costly thin tools when the hole was sufficiently small. However, given both Betty and Abel were wild-caught individuals we do not know how they developed their ability to select and manufacture appropriately-shaped tools, and it is likely to be based on substantial prior trial-and-error/individual learning of hole dimensions and tool sizes, additionally constrained by ergonomic factors.

Field experiments with wild NC crows by Hunt et al. (2006), in contrast, have failed to find similar evidence for spontaneous matching of tools to a given task. Holes of differing depths drilled into the surface of a log, and artificial transparent containers of different depths were presented to two wild NC crows who extracted the rewards with stick-tools or pandanus tools. They found no evidence for a matching of initial tool-length to the task at hand; instead, the authors argue that the crows were using a two-stage heuristic strategy to solve the problem whereby they first attempt to use a default tool, and if that fails they will search for a more suitable (longer) tool. Although the small sample sizes in these competing studies mean that no species-wide conclusions can be formed, it is possible that the wild crows were selecting tools well suited to their daily foraging activities, while the captive crows were not subject to the same degree of tool-size reinforcement, allowing them more freedom in tool choice. Collection of tools left behind in Cerambycid larva burrows at our dry-forest field site revealed a significant correlation between tool length and burrow depth, providing further evidence for tool-size matching in wild NC crows; but the nature of this methodology means we cannot determine what method the crows were using to select their tools (Bluff et al., 2010b).

Rooks are not habitual tool-users in the wild, but captive individuals have recently been reported to show selectivity in tool choice (Bird & Emery, 2009a). This study made use of a collapsible platform holding a reward that could be released by dropping a weight onto the platform through a tube; the rooks were trained to use the apparatus before being presented with an array of tool selectivity tasks. In the first task the rooks were presented with a large or small tube and three sizes of stone (all stones were sufficient to collapse the platform, but only the small stone would fit into the small tube), interestingly three of four rooks successfully chose the small stone in their first trial with the small tube and continued to use large stones when the tube was large; all four quickly adopted this strategy consistently. The rooks were then presented with the small or large tubes, but were required to collect stones from outside of the testing room in the adjoining, visually isolated aviary, forcing them to make a selection based on their memory of the tube size. Again the rooks showed stone size selectivity, although it is interesting to note that they appear to have selected large stones in the first trial irrespective of tube size, and then showed a rapid reversion to small stones for the small tube, with an overall tendency to select smaller stones over the course of the trials irrespective of tube size. Further tasks presented to the rooks are more difficult to interpret given their experience to this point; for example, the rooks were presented with a non-functional round stone and a functional long, thin stone to place into a small tube. However, in 160 trials the round stone was only selected three times and the stone re-orientation required was generally completed at the mouth of the tube opening. The rooks were then trained to use heavy sticks to drop into the tube or light sticks to push the platform down and were then tested on their ability to select between functional and non-functional sticks and stones; i.e. a long, functional stick and large, non-functional stone, or a small, functional stone and a short, non-functional stick. Although the rooks were clearly able to select the functional tool over the non-functional tool, they had received prior training in using the small stone for the small hole and the long stick for pushing down the platform, meaning little can be gleaned from the results. Further tasks involving provision of a novel raw material beside the apparatus also become less informative given the rooks' substantial reinforcement when inserting the provided objects into the apparatus (Seed & Byrne, 2010). For example, in a tool modification task the rooks would insert a branch into the tube and trim off side branches as and when they obstructed the stick's travel. Likewise, a separate study where rooks raised the water level in a clear tube could be explained though this prior training (Bird & Emery, 2009b).

One would generally assume that the performance of humans in these cognition tasks would be highly predictable, but as the trap-tube control example shows this assumption can be flawed (Silva et al., 2005). Silva & Silva (2010) replicated Chappell & Kacelnik's (2002) study with ten humans: a reward (a sweet) was offered at one of two depths in a tube and a number of tools of different lengths were supplied. While the human subjects chose longer tools when the reward was deeper the authors claim that they find no evidence for tool-length matching. Their data show that subjects selected tools *c*. 8cm longer than required, which generally gave a real working length (from finger to tool-tip) *c*. 4cm longer than the reward depth. In my opinion this is an ideal overlap distance with which to retrieve the reward and matching should not have been dismissed so readily in favour of other arguments concerning the number of tools presented of different lengths. Selecting slightly longer-than-required tools is a sensible tactic, particularly given there was little cost in choosing a tool that is slightly longer than required –the longest tool was only 26cm, hardly unwieldy for a human in comparison to an NC crow using a tool as long as its' entire body. This point makes it all the more surprising that the humans did not always select the longest tool – providing powerful support for the theory that subjects were matching the length and leaving a small overlap for ease of use and/or providing room for error.

Humans, tool-using animals and non-tool-using animals alike appear able to select tools of a specific size or shape for a given task, suggesting animals are far better at judging the geometric properties of a task than they are at predicting the course an object will take based on gravity and solidity. Perhaps this cognitive performance is related to an animals' need to forrage for a specific item (e.g. a specific food type) in response to a specific desire or mental state (e.g. specific nutritional demands), building up a search-image for a desired object through individual learning. Animals with greater experience in learning to develop new search-images may be able to form these associations quickly.

9.2.4 Hook Manufacture

The experiments I have reviewed so far have attempted to assess causal understanding in animals by presenting them with tasks that have a limited number of discrete solutions. But instances where an animal spontaneously solves a complex and novel task can be particularly revealing as the feats of generalisation required become increasingly abstract and the chances of random success are far smaller. On the other hand, these observations have no clear null hypothesis, meaning the statistical significance of an animal's performance cannot be assessed. One such example occurred accidentally during the course of an experiment investigating NC crows' ability to select a hooked or straight piece of garden wire to retrieve a bucket in a vertical well (Weir & Kacelnik, 2006). Betty approached the experimental apparatus, but the hooked wire had recently been taken away by Abel (her partner). She attempted to extract the bucket with the straight wire, but when this failed she bent the wire into a hook and used this to extract the bucket (Weir et al., 2002). Although Betty was wild-caught, and possibly proficient at manufacturing hooked stick tools in the wild (Hunt, 1996), it is unlikely she had prior experience with malleable material such as metal wire – particularly in a tool-manufacture context. In subsequent experiments Betty was provided with a new material – malleable strips of aluminium (Weir & Kacelnik, 2006). In previous wire-bending experiments Betty consistently wedged one end of the wire into a crevice and pulled on the distal end. However, the nature of this new material meant her previous wire-bending technique could not be used and she quickly developed a new technique, holding the working (proximal) end of the strip and bending it with her bill. This meant she also needed to flip the tool before use; however, she still attempted to probe briefly with the unmodified end of the tool in five of ten trials. Betty's ability to flexibly alter her manufacture technique and continue using the correct techniques with high fidelity suggests that she was goal-driven to make a hook (which could be taken as evidence for mental representation of a hook), and that the behaviour cannot readily be explained by her prior hooked stick-tool manufacture technique (Hunt & Gray, 2004a). While Betty's repeated attempts to use the unbent end of the tools could refute the notion that she understood the nature of the hook, six to seven year old children will sometimes select a straight pipe-cleaner over a hooked one in an analogous task (Beck et al., 2011). Bluff et al. (2007) present anecdotal evidence that even adult humans likely to be aware of Betty's wire bending sometimes attempt to use the wrong end of a hook-tool they had made seconds earlier. Therefore we cannot use Betty's inefficient hook-tool performance to make inferences about her understanding without first establishing the nature of human mistakes in a similar task.

Further wire-bending experiments were performed to test for Betty's understanding of the nature of malleable materials and how to manipulate them for a specific task, but this time she was required to un-bend tools in order to make them functional (Weir & Kacelnik, 2006).

In the most telling trial, Betty successfully un-bent a u-shaped tool in order to lengthen it and reach the reward; but unfortunately Betty died before further trials could assess her ability fully. Nevertheless, she demonstrated that she could un-bend a tool when required, even though all her previous experience had rewarded bending the material into a hook, further suggesting she was able to design tools to fit a mental representation. Interestingly, captive chimpanzees failed to demonstrate such understanding of abstract concepts in a similar un-bending task, with only one subject of seven managing to modify the material appropriately following extensive additional training in bending tools (Povinelli et al., 2000). Nevertheless, further testing is required to determine whether Betty's performance could be based on prior hooked stick-tool manufacture experience.

Captive rooks in Bird & Emery's study (2009a) were able to spontaneously bend wire into hooks in order to retrieve a bucket at the bottom of a transparent tube – three of four individuals bent hooks and extracted the reward successfully on their first trial. It is important to note that these rooks had up to this point received substantial reinforcement for inserting the supplied material into the tube, to attempt to use both ends of a hooked tool to retrieve a bucket (i.e. flip the tool), and to manipulate the tool at the opening of the tube if it did not appear to work (e.g. they re-oriented stones and pulled side-branches off a stick). The fact that the rooks bent the proximal end of the tool and flipped it, and appeared to bend both ends of the wire could attest to these points. We should therefore be careful in our assessment of the rook's performance, which could possibly be attributed to chaining previous training alone; but there is the additional likelihood that the rooks received prior experience in interacting with malleable steel wire in their aviaries. Indeed, if the rooks, or Betty, had no prior experience in malleable materials they should not be expected to perform so perfectly without some experimentation of the properties of the materials; therefore further studies should determine what other exploratory or motivational behaviours, or prior experience could explain the remarkable performance of these individuals.

9.2.5 Sequential tool-use

Tool-use directed at specific aspects of a task other than the perceived ultimate goal has often been assumed to provide evidence for a greater awareness of the tools' functionality. The use of such 'meta-tools' marked an important evolutionary step in stone-tool manufacturing hominids (Plummer, 2004; St Amant & Horton, 2008), and some argue that the hierarchical planning of skilled feeding techniques (similar to the hierarchical planning thought to underlie meta-tool-use) in great apes could account for the apparent cognitive divide between great apes and monkeys (Byrne, 1997 pp.303-306). However, great care must be taken when considering the cognitive demands imposed by performing an apparently sophisticated and specific sequence of actions, as Epstein (1984) demonstrated effectively when he showed that pigeons could move a box in order to jump up to an out-of-reach reward, similar to the box-stacking ability of chimpanzees in Köhler's (1925) study. Epstein achieved this by training the pigeons in each step of the task separately, and when given the opportunity the pigeons would chain the actions together to perform an apparently insightful sequence of actions. The propensity for chaining together behaviours acquired through individual learning – manifesting as apparently complex and insightful behaviours – means that wild observations cannot be taken as reliable evidence for causal understanding. Perhaps the closest wild example of such planning is found in chimpanzees foraging for termites or honey; they have been observed to use a ‘tool set’, first using a large stick to break into the mound or hive, and then using a flexible, slender tool to extract termites or honey (Brewer & Mcgrew, 1990; Bermejo & Illera, 1999; Sanz & Morgan, 2009). All of the tools in chimpanzees’ tool sets are directed at the reward or goal, but instances where a tool is directed at manufacturing or acquiring another tool (defined as ‘constructive’ and ‘sequential’ tool-use respectively by Wimpenny et al. (2009)) require a greater level of abstraction that makes chaining less plausible. Constructive tool-use has only been documented in hominids (e.g. Plummer, 2004), but spontaneous sequential tool-use has been reported in a number of captive non-humans including chimpanzees (Köhler, 1925), orangutans and gorillas (Mulcahy et al., 2005), capuchins (Anderson & Henneman, 1994), rooks (Bird & Emery, 2009a), and NC crows (Taylor et al., 2007). Taylor et al. (2007) use an experimental design typical in these studies; showing that NC crows could spontaneously use a short tool in order to retrieve a long tool that enabled them to reach a food reward in a tube; claiming that this demonstrated analogical reasoning in NC crows (i.e. they understood that just as tools can retrieve food, they can also retrieve tools). However, such reasoning by analogy can boil down to a simple generalisation that inaccessible, desirable objects can be reached with tools (e.g. Clayton, 2007); a heavily reinforced principle in NC crow behaviour. In many of these studies there were insufficient controls to determine how the animals were solving the tasks. For example, Mulcahy et al. (2005) only offered one out-of-reach tool, so the subjects’ acquisition of this tool could have simply been attributed to displacement behaviour. Taylor et al. (2007) attempted to remedy this by offering two out-of-reach objects; a long tool and a stone. However, this is an entirely uninformative control given the difference in salience between the stick tools they use every day to acquire food, and an ecologically irrelevant stone that they would rarely chose to interact with, even in captivity. A far more suitable control would have been a short tool, but even this would not rule out the use a previously reinforced search image for a suitably long tool. Bird & Emery (2009a) provide a better control, offering two out-of-reach stones that had both previously been rewarded, also avoiding the ecological salience problems caused by using sticks with NC crows. However, the rooks' sequential tool-use performance in this study could simply be attributed to their prior training for inserting objects into the holes provided. Likewise, in many previous experiments (e.g. Mulcahy et al., 2005; Taylor et al., 2007) the subjects had previously been trained in the individual steps in this task, including presenting them with the long tool in the position where it would later be out-of-reach, and training them to use the long tool to retrieve the reward; as such simple chaining could not be ruled out (see Clayton, 2007; Wimpenny et al., 2009).

Wimpenny et al. (2009) present data from two experiments specifically designed to probe how NC crows solve sequential tool-use tasks. Rather than presenting just one out-of-reach tool, multiple tools of different lengths and functionality were supplied; additional controls included an absence of a food reward, no requirement for sequential tool-use, manipulation of the pre-training subjects received, and even a requirement for using three tools sequentially. All three subjects that were given prior training in the use of a tool provided in horizontal tubes (like the prior training in Taylor et al., 2007) spontaneously solved the sequential tool task on their first trial, while only one of three subjects that had not received prior training learnt to solve the task slowly, taking over 20 trials. This suggests chaining could have accounted for the spontaneity of sequential tool-use observed by Taylor et al.

(2007). However, in the second experiment – which avoided the potential visual problems created by acrylic tubes by using a wire cage – all three subjects spontaneously solved the sequential tool-use task, including one that had not participated in the previous experiment. All three subjects were also able to use three tools sequentially, a feat far less likely to occur by chance than the two-tool sequence. Two of the subjects also extracted tools that were longer than expected by chance, and there was a tendency to swap short tools for long ones, but not the reverse. Nevertheless, Wimpenny et al. (2009) do not rule out low-level explanations for the observed behaviour arguing instead that the subjects were likely to have made a general assessment of the situation in each trial, for example, determining presence/absence of tools and reward, and whether the reward is within reach with the currently available tool. When the situation is unclear the crows will attempt to use the tool they currently have, and only change strategies if this fails (i.e. similar to the two-stage strategy proposed by Hunt et al., 2006).

Taylor et al. (2010a) present data from an follow-up sequential tool-use puzzle that controls for the subjects' prior experience, attempting to rule out chaining and conditional reinforcement (e.g. crows associate tools with a reward, so tools are desirable objects in their own right). In this study NC crows were required to pull up a short tool suspended from a string, use this short tool to retrieve a long tool, and then access the reward. Four crows were pre-trained on all components of the task excluding the use of a short tool to access a long tool, and pulling up string with a functional tool on the end; a control group of three subjects was pre-trained on all components including these two conditions. In one of the pre-training tasks (provided to each individual twice) the crows were presented with a non-functional 5cm tool with which to extract a 15cm deep reward, and in another they were simply required to pull up a string with meat tied to the end. All three crows that were pre-trained in all steps of the task unsurprisingly chained these actions together in the first trial of three-stage testing. One of the four subjects that had received pre-training in all tasks except pulling up a tool on the string and using a short tool to access a long tool also successfully completed the first trial of the three-stage task, and the other individuals were successful within four trials. The success of individuals in this latter group led Taylor et al. (2010a) to conclude that the crows' "performance was consistent with the transfer of an abstract causal rule: 'out-of-reach objects can be accessed using a tool'" (Taylor et al., 2010a, p.1). However, there are two reasons to doubt the successful crow's performance: (i) the crow had previously been trained to pull up string to access a reward. Given a choice NC crows will tend to pull up a sting with meat on the end more frequently than a stone, but nevertheless they will occasionally pull up non-salient stones (Taylor et al., 2010b). In this sequential tool-use experiment they had no choice, so either displacement or prior training could well account for their retrieval of the short tool. (ii) It is likely that the short tool was not the conditional punisher it was claimed to be by Taylor et al. (2010a). Two unsuccessful trials are unlikely to undo a lifetime of reinforcement and inherited predispositions for a desire to access tools – even short ones.

Irrespective of these considerations I would contest the level of abstraction required in these sequential tool-use tasks. This all hinges on how abstract the generalisation is that 'tools can be used to access inaccessible objects'. While Taylor et al. (2010a) argues that this represents a high level of causal understanding I see this as a fairly rudimentary generalisation, particularly given the neophilic nature of NC crows and their tendency to approach novel problems with a tool (Auersperg et al., 2011; Wimpenny et al., 2011). Assuming NC crows treat tools as an extension of their bodies (e.g. through motor learning and body 'schema' (Maravita & Iriki, 2004)), then the realisation that tools can be used to access out-of-reach objects becomes akin to picking up an object that is within their reach. The results of all of these sequential tool-use studies could be explained by two additional simple associatively learnt and ecologically plausible means: (i) a general desire for all potential stick material - as shown by the crows in Wimpenny et al. (2009) that extracted the long tool when no food was supplied; and (ii) tool length selectivity (discussed above), and/or a preference for longer sticks, possibly based on a search image. This last point is supported by our evidence from the field that shows NC crows select tools that are longer than the average raw materials available (Bluff et al., 2010b).

9.3 Summary

There is currently little evidence for high-level cognitive abstraction in non-human animals, nor is there support for the notion that tool-using animals may understand physical causality better than non-tool-using animals. This refutes suggestions that advanced physical intelligence evolved to facilitate tool-use (e.g. van Schaik et al., 1999). Instead it would appear that many intelligent animals – such as corvids – are cognitively equipped to judge the geometric dimensions of a task and rapidly decide which tool to use based on prior experience (Chappell & Kacelnik, 2002; Chappell & Kacelnik, 2004; Bird & Emery, 2009a). Such spatial awareness in conjunction with other individually learnt mechanisms and simple generalisation could account for almost all of the behaviour reported in non-humans (although what counts as a 'simple generalisation' as opposed to advanced analogical reasoning will always be contentious). Indeed, most human behaviour seems to rely on similar principles – the vast majority of human behaviour is habitual (how many times a day, or even a year do we adult humans learn a completely new skill?) and essentially all human professions and skills require considerable prior training. The reliance of human culture and professions on high fidelity imitation and occasional innovation (rather than true invention) is readily evidenced in our slowly evolving material culture both in the fossil record and throughout recorded history. Further work in this area should compare human and non-human individual learning and generalisation more explicitly; perhaps we simply use a faster form of individual learning than non-humans based on additional experience in learning to use associative learning or other forms of individual learning and generalisation. If so, then investigating the motivational factors that promote ‘learning to learn’ should be investigated in comparative non-verbal studies, for example: patience during problem-solving, exploratory play, directing attention, neophilia, and a rapid ability to inhibit ones’ actions. Although current data suggest non-humans are unable to mentally simulate gravity and solidity, we can never rule out higher-level abstraction in non-humans (Bluff et al., 2007). The paradigms used to test for this ability in non-humans have highlighted methodological problems, many of which have not been satisfactorily resolved. I therefore devised a novel alternative to the trap-tube that could solve many of these problems, while improving accessibility to non-tool-using species.

10 CHAPTER TEN – SEE-SAW PARADIGM

10.1 Introduction

The trap-tube paradigm has turned out to be more of a problem-solving activity for humans than the animals it has attempted to test (see section 9.2.1). Recent experiments have required a whole host of control conditions to rule out simple associatively learnt rules (e.g. Seed et al., 2006; Taylor et al., 2009b), meaning the subjects' immediate response after mastering the initial trap-tube experiment could be lost as they attempt to form new rules. Additionally, the basic mechanics of the apparatus have proven highly problematic – animals would much rather pull a reward towards themselves than push it away (Tebbich & Bshary, 2004; Mulcahy & Call, 2006). Eliminating the need for tool-use entirely can further reduce the complexities of the task (Seed et al., 2009), while also making it accessible to non-tool-using species (Seed et al., 2006; Teschke & Tebbich, 2011). One last problem is illustrated by the capuchin and woodpecker finch that solved the trap-tube (Visalberghi & Limongelli, 1994; Tebbich & Bshary, 2004); these subjects would push the reward slowly and change sides repeatedly, reversing direction only when the reward nearly tipped into the trap. In order to compare the physical cognition of tool-using and non-tool-using species I have devised a novel alternative to the trap-tube task that solves these issues.

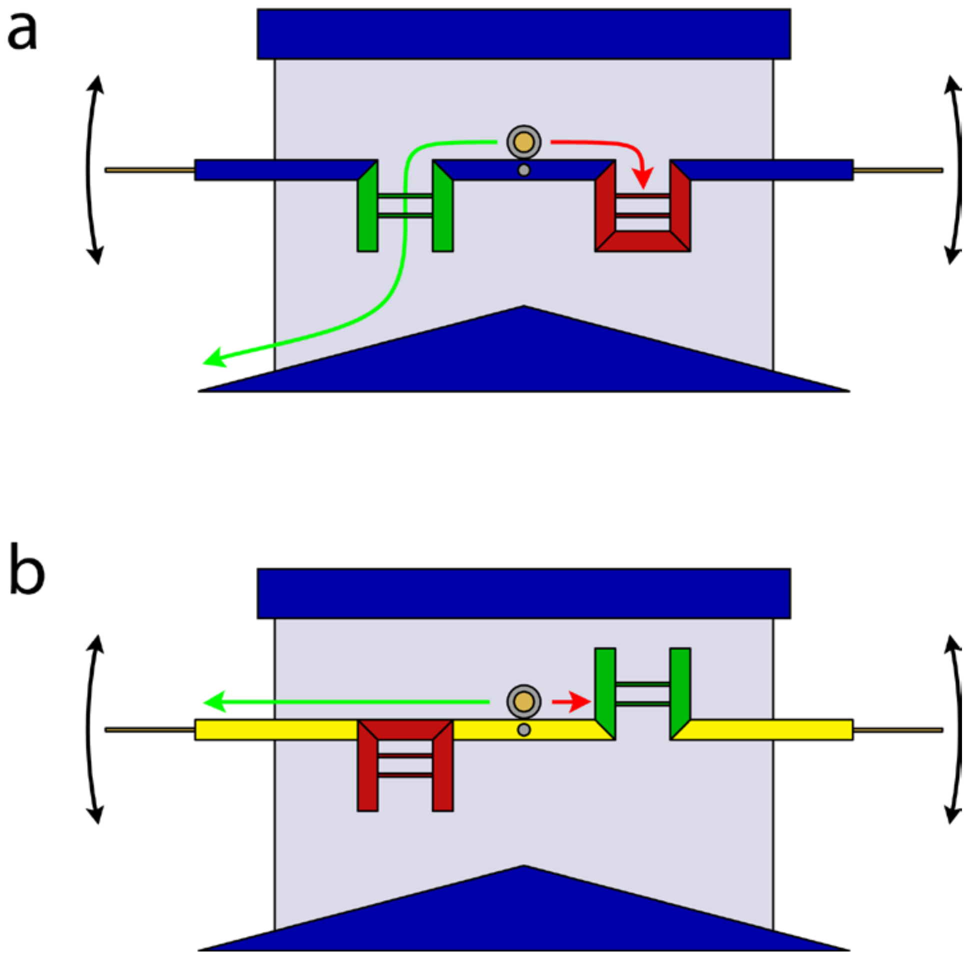

Figure 10-1. See-saw experimental paradigm illustration. The see-saw pivots in the middle, so subjects can pull down or push up either end to set the reward rolling; green arrows show the correct path, and red arrows show the incorrect path.

The see-saw task (shown in Figure 10-1) is mechanically accessible to any animal that can press or lift a lever, has a single control condition that would immediately rule out almost all associatively learnt cues, and once the reward starts moving it is difficult to change direction. In the initial see-saw trials (Figure 10-1A) subjects must roll the reward through an open hole, avoiding a pit-trap with a closed hole. Once subjects reach the criterion for success in this task they are transferred to the control task (Figure 10-1B). This control flips both the trap and hole upside-down, reversing their functionality and controlling for all potential cues, such as causally irrelevant colour and surface continuity. Captive rooks have recently been found to be capable tool-users in specific contexts (although see section 9.2; Bird & Emery, 2009a), suggesting that cognitive ability is not a limiting factor in non-tool-using species adopting tool-use. The see-saw apparatus is ideal for comparative testing of tool-using and non-tool-using species to determine whether they have different levels of physical cognition with regard to object solidity and gravity. A recent study compared exploration and physical cognition in NC crows and kea using a puzzle box that offered subjects four potential means for accessing the reward. This experiment found that NC crows tended to use tools wherever possible, and were less able to discover new solutions to the puzzle box as rapidly as the kea. Ultimately one kea (of six) and one NC crow (of five) mastered all four solutions, suggesting that both species are comparably able in terms of physical cognition, but vary considerably in their exploration tactics. Parrots and crows are both generally accepted as intelligent, proportionately large-brained bird taxa (Emery, 2006), yet they are phylogenetically extremely distant from one another (Hackett et al., 2008). They are therefore ideally placed for comparative studies looking at whether their advanced levels of cognition evolved as specialised domains, or whether both rely on generally heightened abilities in all areas. As such I tested the see-saw paradigm on NC crows and red-fronted parakeets *Cyanoramphus novaezelandiae* (named ‘kākāriki’ by the Māori, and ‘kakariki’ hereafter).

10.2 Methods & Results

Two NC crows and one kakariki were presented with the initial see-saw task. Each subject completed 100 trials, but none of the subjects reached criterion for progressing to the control condition (success in 9 or more out of the last 10 trials, i.e. a cumulative probability of 0.012). The see-saw apparatus was positioned at a random orientation (determined by spinning a marked coin), and subjects were allowed to access the apparatus for 5 minutes. If the subject pushed down or pulled up one end of the see-saw so that the reward fell into the hole or trap the trial was scored as a success or failure respectively. If the subject did not interact with the apparatus within five minutes the trial was discounted. In either scenario a new trial was presented 10 minutes later, with up to 10 trials per subject a day. All trials were recorded using a Sanyo Xacti HD2000 video camera. I tested one captive NC crow (‘Uek’) in Germany (Figure 10-2A); she was presented with dead meal-worms held in a round plastic holder in the centre of the see-saw and quickly discovered that pushing down or pulling up one end of the see-saw would release the reward. Although there was no clear side-bias, and she was clearly frustrated when the reward fell into the trap she did not improve beyond chance levels of success. The second NC crow tested was a wild-caught female (based on Kenward et al., 2004), captured at our Gouaro-Déva dry-forest study site and housed temporarily (for 3 weeks) in an 18m^3 aviary before being released. Wild NC crows appear to habituate to temporary captivity exceedingly well, and this technique has been used extensively by the Auckland based group (e.g. Taylor et al., 2007; Taylor et al., 2009b; Taylor et al., 2010a). The subject was offered re-hydrated cat-food daily, with additional pieces of beef heart hidden around the aviary. She was initially wary of the see-saw apparatus, so I extended the see-saw arms with 12cm lengths of bamboo skewer; in pre-testing I skewered pieces of beef heart on both ends of the see-saw, so that attempting to remove them would dislodge the reward (a *c*. 1cm^3 piece of beef heart held in a round plastic holder). She quickly learnt to push down on the see-saw arms and progressed to testing, but she showed a clear side-bias, almost always pushing down on the end nearest the centre of the aviary (Figure 10-2B). The kakariki (approximately 9 months old and probably male given bill shape) was tested within a mobile testing trolley adjoining its aviary (Figure 10-2C). The trolley had a waiting chamber 60x60x120cm, from which the subject could see his parents and siblings, and a testing chamber 60x60x60cm, visually separated from all other individuals, accessed through an experimenter-operated sliding door. The reward was a round core of cooked carrot 10mm long by 8mm diameter, dipped in a few grains of sugar and delivered within an aluminium tube. Pieces of cooked carrot were attached to both skewer arms in pre-testing similar to the beef pieces with the wild NC crow. This kakariki also developed a side-bias, tending to push down the end nearest one corner of the testing chamber. See Figure 10-3 for trial outcomes in the initial see-saw testing.

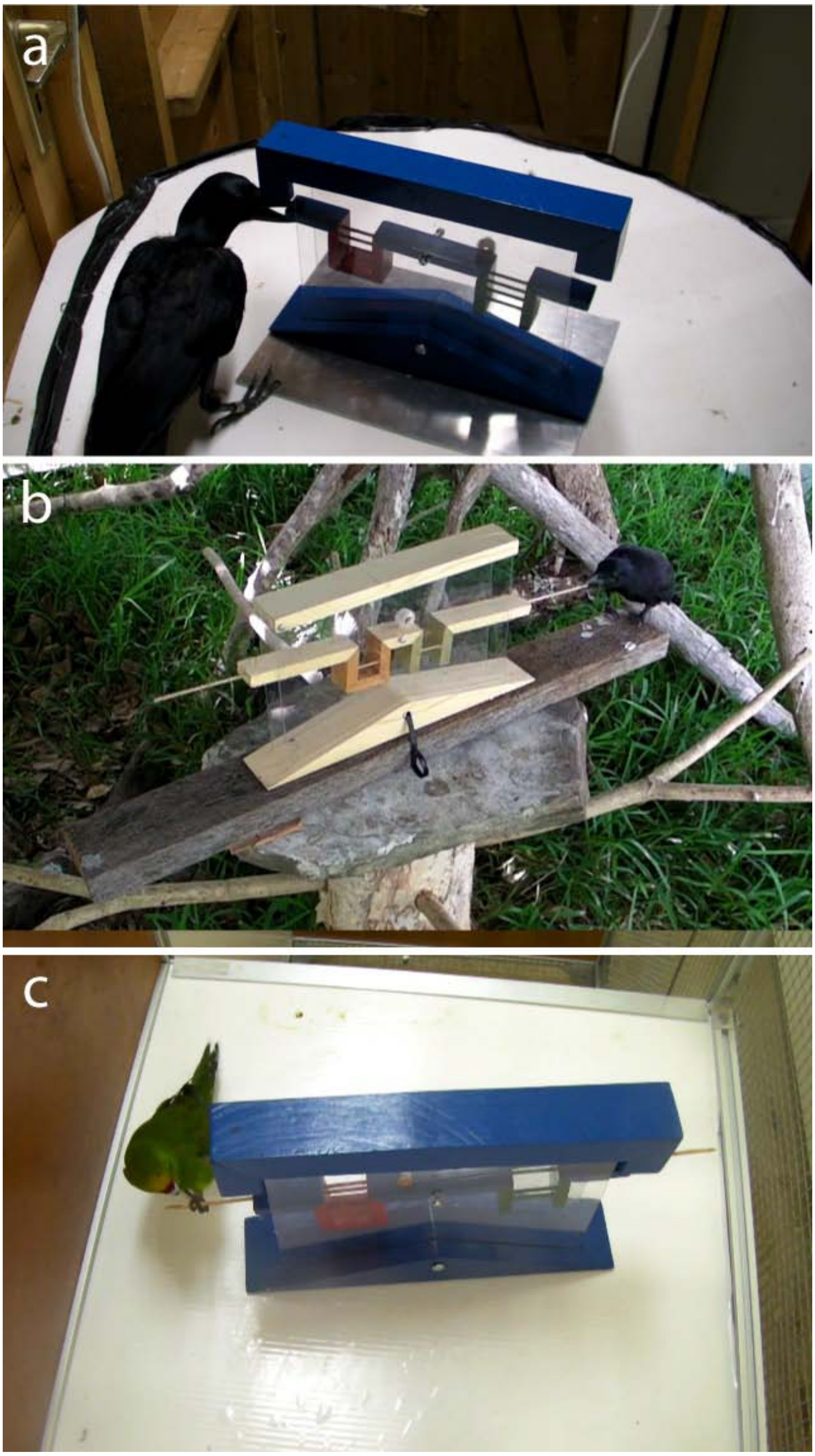

Figure 10-2. Still-frames taken from video footage of see-saw trials with a captive NC crow (Uek) (a), a wild-caught NC crow (b), and a captive kakariki (c).

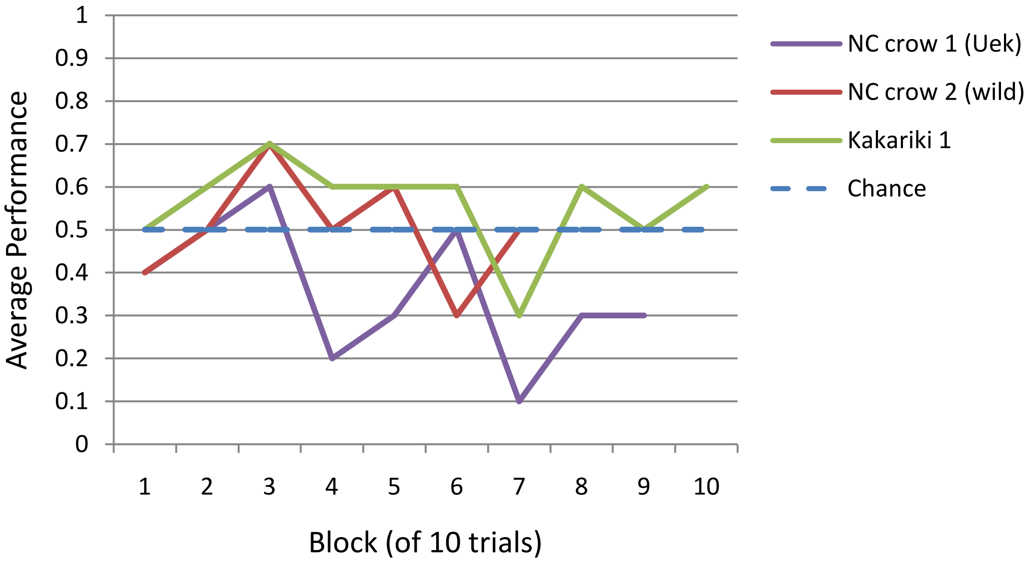

Figure 10-3. Results of initial see-saw trials on three subjects: two NC crows and one kakariki. None performed above chance level, and two developed clear side-biases.

10.3 Discussion

None of the subjects in my experiment successfully passed the initial see-saw task. All three subjects demonstrated apparent frustration when the reward became trapped (e.g. aggressively tapping at the transparent wall adjacent to the reward), and in initial trials they all walked around the apparatus, visually inspecting it before interacting. Nevertheless, none of them learnt to perform above chance and two developed clear side-biases. Given the low sample size it is difficult to determine the reasons for the subjects' performance. It is possible that the two ends of the see-saw were not sufficiently visually distinct, so the subjects failed to differentiate between them and reverted to a random tactic, or rules based on position (causing a side-bias). Additional pre-testing experience of using a plain see-saw (i.e. a simple, continuous surface without traps and holes) could aid the subjects' ability to learn about the characteristics of the see-saw's moving surface and the associated movement of the reward. A somewhat similar see-saw task was presented to woodpecker finches and small tree fiches with a trap central, food offset layout or vice-versa; five of six small tree finches successfully learnt to perch on the end of the see-saw that tipped it in the correct direction, and two of twelve woodpecker finches solved the task. However, none of these subjects passed a control test where the reward and trap positions were reversed (Tebbich et al., 2010). Had the subjects passed the see-saw test used by Tebbich et al. (2010), their experimental design meant that surface continuity could have been used as a cue (though a causally relevant cue), thereby preventing clear conclusions regarding physical understanding. Nevertheless, the ability of the Darwin's finches to successfully learn how to use the see-saw in their first task suggests the see-saw itself should not pose a problem for NC crows and kakariki.

Further testing with a larger sample of NC crows and non-tool-using birds such as parrots and other Corvidae would be needed to determine whether this paradigm could be a simple alternative to the latest trap-tube methodology (Seed et al., 2006; Taylor et al., 2009b; Teschke & Tebbich, 2011). But as it stands little can be inferred from these results.

11 CHAPTER ELEVEN – CONNECTIVITY TEST

11.1 Introduction

Sequential tool-use tasks appear to show that New Caledonian crows can generalise the principle that just as tools can be used to reach inaccessible food items, they can be used to access non-food items that are otherwise out-of-reach (see section 9.2.5; Taylor et al., 2007; Wimpenny et al., 2009; Taylor et al., 2010a). In humans and perhaps some other primates our brains start to treat tools as physical extensions of our own bodies as we use them, altering our body 'schema' to account for the spatial changes (Maravita & Iriki, 2004). If NC crows rely on similar body schema that are somewhat hard-wired then they might not need to rely on a generalisation to realise that tools can grant them access to out-of-reach objects, changing the task to an awareness of the affordances of one's body plan. Connectivity has been used to test animals' physical understanding in a multitude of ways (see section 9.2.2), and NC crows, ravens and even goldfinches and siskins can spontaneously pull up a reward hanging from the end of a line (Heinrich & Bugnyar, 2005; Seibt & Wickler, 2006; Taylor et al., 2010a). Initial learning of the string-pulling task could be explained by an attempt to reach directly towards the reward, biting at its vicinity and realising that the reward comes closer when the string is pulled. However, the rapid performance of NC crows and ravens in this task implies they appreciate the level of connectedness between the string and reward, and pull up the reward correctly from their first attempt. Demonstrating that any animal understands the connectivity between objects that are not attached directly with a straight section of line is more difficult, particularly when they have received prior training in string pulling (Heinrich & Bugnyar, 2005).

In order to test whether NC crows automatically treat tools as extensions of their own bodies I presented a novel and simple connectivity problem. A reward was left hanging on a line near a perch so that the line was just out of reach, and the reward was suspended below the perch. An NC crow with a tool would be able to reach the line easily and pull it in, but would not be able to reach the hanging reward with ease. This is a simple form of sequential tool-use requiring an understanding (or ability to generalise) in areas that most crows have proven instantaneous correct performance, i.e. sequential tool-use and string pulling.

11.2 Methods

The first string-pulling test was positioned in Gouaro-Déva; our dry-forest study site on Grande Terre at coordinates -21.556246°S, 165.315458°E in conjunction with the first larva-cam experiments (see section 4.2). An ‘F’ shaped wooden frame was secured in the ground *c*. 7 m from a hide. The upper bar of the F-frame was 123 cm above the ground and a length of fishing line was attached at the top (see Figure 11-1a). The shorter central bar provided access to the hanging line so that it was 30 cm from the end of the perch to the line. Larvae were attached to a noose on the end of the line so that the larvae hung below the central bar. This apparatus was first presented to wild crows on 26 November 2007, alongside larva-cam, but fieldwork was disrupted due to rain until 9 December 2007. After this the experiment ran continuously alongside larva-cam testing until 21 December 2007.

The second string experiment was positioned *c*. 15 m from the previous string test, run from

5 December 2008 to 20 December 2008 inclusive alongside an experiment that required wild NC crows to extract pieces of beef heart from a provisioned log using stick-tools. This time pieces of beef heart *c*. 1 cm^3 (rather than larvae) were suspended from a weak, inaccessible branch in a tree c. 5 m from a hide. The line passed within 30 cm of a horizontal branch that was easily accessible to the crows. However, a crow managed to pull up the larva from the weak branch attachment in this position, so instead a second overhead line was tied between two branches and the line holding the bait was suspended from this, preventing the crows from accessing the top of the line (see Figure 11-1b). After successfully retrieving the bait the apparatus was refreshed five minutes after the subject left the vicinity of the hide and any tools used were collected.

All events were recorded with a video camera and high-resolution photographs were taken in order to identify unmarked individual crows based on their unique leg scale markings (see section 4.2).

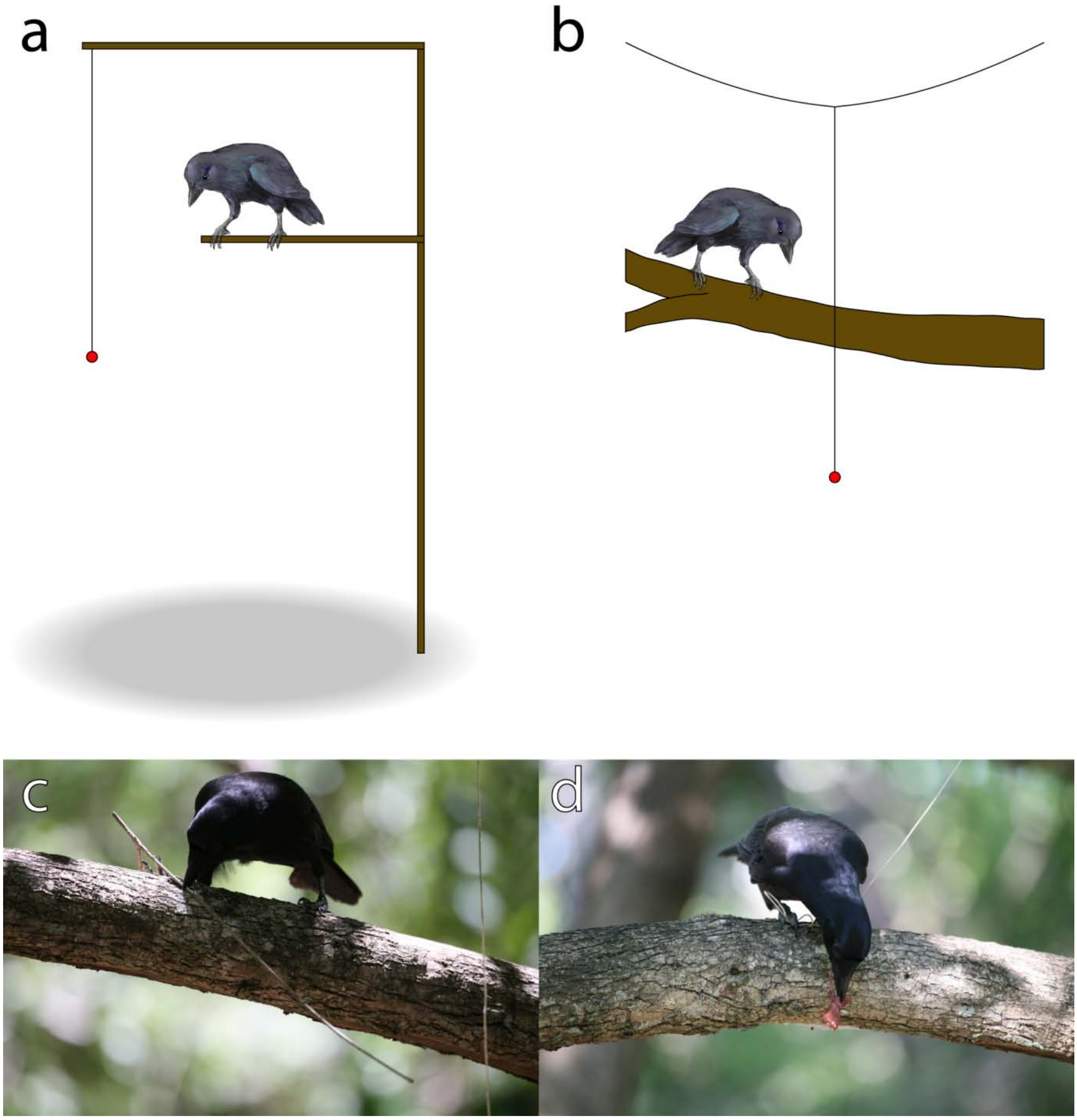

Figure 11-1. Schematic of the connectivity test. a) An illustration of the ‘F’ shaped wooden frame with an out-of-reach reward (red) suspended on a string from the upper bar; b) the out-of-reach line suspended from an overhead line to prevent subjects from pulling up the reward. c) A photo of the subject manipulating a tool next to the line. While this tool is easily of sufficient length to reach the string the subject did not direct the tool at the line or reward. d) Subject retrieving the bait on the end of the line after developing a successful strategy that did not require tool-use.

11.3 Results

There was little interest in the first experiment; two crows briefly perched on the upper bar of the F-frame, and one attempted to reach the larva by jumping from the ground. However, none were successful in accessing the larva.

The second experiment attracted considerable attention from one individual ('UC2' from the larva-cam experiment, see section 4.2). On 5 December 2008 UC2 managed to access the top of the string where it was attached to a small twig; on the first attempt UC2 lost its footing and flew to the ground, and on the second attempt UC2 managed to pull up the string and retrieve the reward. The next day the string was attached to an overhead line so that the crows could not access the top of the line. UC2 investigated the point where one end of the overhead line was attached to the tree, repeatedly pecking at the knot and pulling at the loose end. On 8 December 2008 UC2 attempted to dive at the reward, but failed, and a few minutes later perched adjacent to the line with a stick-tool in its bill but it did not attempt to reach for the line with the tool. UC2 returned later the same day and again attacked the knot where the overhead line was attached to the tree, this time with greater force. Approximately two hours later UC2 returned to the perch with a stick-tool in its bill, but dropped the tool without attempting to reach for the line (see Figure 11-1c). On 9 and 11 December 2008 UC2 made further attempts at working on the point of attachment of the overhead line and returned to the perch with a stick-tool but did not use it. On 14 December 2008 UC2 attempted to jump at the reward from the ground, then tried to reach for the reward from the perch, and then flew at the reward from the perch. Although UC2 did not mange to catch the reward this did cause the line to start swinging. UC2 immediately flew back up to the perch and caught the line as it swung near, UC2 pulled up the bait with its bill and securing the line under its foot (see Figure 11-1d). UC2 repeated this method 15 minutes later (set the line swinging, then catch it), and continued to use this method, once on 15 December 2008, and again on 16 December 2008. On 28 December 2008 (i.e. eight days after the connectivity test had ceased to be baited) UC2 again attacked the knot attaching the overhead line to the tree.

11.4 Discussion

Although a sample size of one is insufficient for generalisations about all NC crows' understanding of tool-use and connectivity this experiment presents an interesting finding. The most telling observation is that the subject repeatedly perched within *c*. 40 cm of the line with a suitable stick tool in its bill but made no attempt to use the tool in order to reach the line. This was not for want of a desire to reach the line without a tool, the subject repeatedly attempted to grab the line from the perch and these actions were not directed down towards the reward. This indicates the subject demonstrated an awareness of the connectivity between the line and reward, and even successfully pulled up the line from the top on its second attempt (note that the first attempt would probably have been successful if the line weren't attached to the tip of a thin branch that barely supported the crow's weight). When the line was later suspended from a second overhead line the subject immediately started pecking at the attachment point of the overhead line. While this could demonstrate an understanding of the indirect connectedness of this line to the reward, it could simply manifest as an interest in the knot itself as a novel material. Indeed, eight days after the apparatus had ceased to be baited the same individual returned to peck at the knot, suggesting it was an interesting object in its own right. After numerous failed attempts at grabbing the line the subject stumbled upon an elegant solution: it flew directly at the reward (probably as an initial attempt to grab it mid-flight), which set it swinging, then it flew back up to the perch and grabbed the line as it swung near. The subject became adept at this solution rapidly, at least demonstrating a quick ability to respond to the new affordances of the swinging line and learning from its previous activities.

This provides evidence that at least one NC crow does not apparently alter its body schema when holding a tool. Gathering data from more individuals would be beneficial as this outcome is somewhat surprising given the NC crow's tendency to approach novel problems with tools (Auersperg et al., 2011; Wimpenny et al., 2011). However, if all NC crows show the same type of performance this has an interesting bearing on the sequential tool-use studies, suggesting that they are indeed using a higher level cognitive generalisation that tools can be used to access out-of-reach desirable objects, rather than body schema, which is perhaps a more neurologically simple explanation. While the subject was probably an immature adult based on gape colouration (Rutz et al., 2010), there is no reason to think its tool-use behaviour was substantially below average for its age, and there is some evidence that it was slightly less sensitive to the weight of larvae in the larva-cam experiment (see section 4.3). Nevertheless, an alternative hypothesis is that a flexible body schema that accommodates its plan for tool-use takes a number of years to develop in young NC crows. This could help explain the long period of high individual and parental investment in tool-use (Bluff et al., 2010b; Holzhaider et al., 2010b).

12 GENERAL DISCUSSION

The data I have presented in this thesis builds upon our knowledge of the behavioural ecology, morphology and cognitive abilities of New Caledonian crows, helping us to understand how and why tool-use has evolved in this species. Although we can never wind back time to investigate exactly how tool-use was selected for in the NC crows' ancestors, and there is little hope for discovering fossil evidence that could help answer this question (see section 8.4), my work does shed light on the possible timing and rate of evolution of tool-use. The revelation that our extensively studied dry-forest crows manufacture hook tools for foraging in paperbark trees suggests that the introduced candlenut tree is unlikely to have played as prominent a role in the evolution of NC crow tool-use as native florae and faunae. This could rule out the need for an incredibly rapid evolution of tool-use in response to human settlement as had been previously suggested (Rutz et al., 2010). Nevertheless, there is reason to believe that NC crows' tool-use evolved under considerable selection pressure, undergoing faster evolutionary rates of change of binocular overlap than any other species modelled. This selection pressure has resulted in the largest binocular overlap in any bird species measured to date, which combines with their straight bills to facilitate a secure grip on the tool in addition to superior visual guidance. Not only is this the only evidence for tool-related morphological adaptations in a non-human, it could also help account for the apparent scarcity of tool-use in other crow species.

It was often supposed that tool-using animals required specialised cognitive adaptations to aid their understanding of the tools they used (e.g. van Schaik et al., 1999), however, a recent study found that captive rooks could become proficient tool-users (Bird & Emery, 2009a). This suggests that animals recognised as being generally intelligent (or those with proportionately large brains), such as corvids (Emery & Clayton, 2004) may already be cognitively equipped to use tools. By modelling the ability of a number of corvids to hold and visually guide a tool I have shown that non-tool-using species would encounter difficulties should they attempt to use a stick to extract something from a hole. This form of extractive tool-use is one of the most important modes of tool-use found in chimpanzees and woodpecker finches and it allows the animals to access food sources that would otherwise require morphological specialisations, such as those of woodpeckers, anteaters or aye-ayes. Parrots are another intelligent group of birds that do not habitually use tools in the wild (although see Borsari & Ottoni, 2005), but – like the rooks – are able to do so in captivity (Auersperg et al., 2011). It remains to be seen whether similar morphological impediments could limit parrots' expression of tool-use in the wild, but my research has also revealed a behavioural aspect of tool-use likely to account for its scarcity in wild populations.

Young NC crows appear to spend years honing their tool-use skills (Bluff et al., 2010b), burdening their parents during their slow development (Holzhaider et al., 2011). The larva-cam experiment helped to explain how an apparently simple tool-use task can require subtle tactics that each crow must learn alone. Not only could this provide a plausible explanation for their slow development of tool-use proficiency in the wild, it also highlights the substantial investment in learning required by this foraging mode. Tool-use behaviour in NC crows is thought to develop from inherited stereotyped behaviours, exposing juveniles to learning conditions that promote the mature, sophisticated and flexible tool-use that manifests in adults (Kenward et al., 2006). Such precursor behaviours have been observed in other tool-using species, such as Egyptian vultures *Neophron percnopterus*, which throw small eggs at stones and later learn to use the same movements to throw stones at large eggs in order to break them (Alcock, 1970). Hunt & Gray (2003) speculate that a tendency to rip at the base of *Pandanus* spp. leaves while foraging could be a precursor for pandanus tool manufacture in NC crows, although parental niche construction is also likely to play a role (Holzhaider et al., 2010a). A recent comparative analysis found that the precursors for caching behaviour in ravens are similar to the precursors for tool-use behaviour in NC crows (Kenward et al., 2011). Ravens have even been observed caching non-food items such as sticks. An interesting hypothesis proposed by Kenward et al. (2011) is that the NC crows' ancestors might have cached sticks in burrows, but due to lack of specialised extractive foragers in New Caledonia, if the stick were then withdrawn it might well tease out an invertebrate, granting the subject privileged knowledge of the potential foraging opportunity. This form of precursor behaviour is unique to caching species such as corvids, and analogous sources for precursor behaviours in the woodpecker finch remain unknown, but nest building could offer the required object manipulation and combination skills (Hansell & Ruxton, 2008). Kacelnik (2009) suggests that NC crow tool-use may depend upon motivational desires to perform specific object oriented actions; however the finding that there is little difference between young raven and NC crow object combination frequencies indicates that this is not quite the motivation that drives tool-use. Instead, Kenward et al. (2011) argue that behavioural persistence seems to be important as NC crows continue to manipulate objects for longer than ravens, and in the wild young individuals continue probing for larvae unsuccessfully for many hours (Bluff et al., 2010b).

Thus, corvids seem perfectly positioned to become tool-users. They are likely to possess the necessary precursor behaviours (Kenward et al., 2011) and sufficient ‘understanding’ for tool-use (Bird & Emery, 2009a), changing the question to why tool-use is so infrequently seen in these species. The findings I have presented in this thesis help to explain why it is unlikely that these apparently well equipped corvids would ever use tools; the initial investment in tool-use, spurred by motivation for persistence is presumably extremely costly, resulting in incredibly slow rates of tool-use development (Holzhaider et al., 2010a). My data suggest even a simple larva extraction task is likely to require a high level of repetitive exposure to learning opportunities. A second major cost is the morphology associated with tool-use. The general corvid lifestyle is suited to probing in substrates for food, tearing flesh from carcasses and then caching the excess away from pilferers. However, the bill morphology associated with this foraging mode is poorly suited for extractive tool-use, and a straightening of the bill like that of the NC crow might render them less competitive at scavenging and probing with the bill (Kulemeyer et al., 2009).

My morphological data provide another speculative hypothesis for the evolution of tool-use in NC crows that is not mutually exclusive from the aforementioned behavioural hypothesis. The unique ecological setting in New Caledonia resulted in decaying wood and crevices that would have harboured a valuable but well protected food resource. The ancestral NC crow would have been able to access a small portion of these dense invertebrate populations at the extremities of logs and crevices by breaking off weak sections of decaying wood. A curved bill is poorly suited for transmitting forces in a woodpecker-like action, and any straightening of the bill would increase the pecking force available to the crows and their ability to access this resource, gradually selecting for a straightening of the bill. Anecdotal evidence shows that NC crows are able to strike deadwood with considerable force (see Figure 12-1), and it would be interesting to compare the skull anatomy of NC crows and other *Corvus* species do determine whether they have woodpecker like skull adaptations for transmitting and dissipating impact forces (Bock, 1999). Once the bill was sufficiently straight my data and evidence from rooks (Bird & Emery, 2009a) suggest the crows would be fairly well disposed to use tools for extractive foraging (as hypothesised by Kenward et al., 2004; Kenward et al., 2011), readily maximising their reach into deadwood in a fashion similar to the woodpeckers' tongue (Cartmill, 1974; Bock, 1999; Villard & Cuisin, 2004).

Figure 12-1. Photograph of an NC crow pecking at deadwood with substantial force. I took this photograph at a log provisioned with larvae positioned next to a hide at 08:52 on January 10 2009 using my Canon 5D DSLR with a Canon 100-400mm 'L' lens.

The picture forming of NC crow tool-use evolution is one of specific, yet subtle motivational and morphological changes. There is no reason to believe there are any specific differences in causal understanding between tool-using and non-tool-using corvids. While much of the research into causal cognition continues to focus on human-like levels of ‘understanding’ in other animals without addressing whether humans would even understand the problem in practice, more fruitful research has highlighted the conditions that cause different species to tackle the same problem in different ways, or behavioural differences that expose subjects to suitable learning conditions. The NC crows’ evolution of sophisticated tool-use without any apparent increase in brain capacity, general intelligence, or even object-specific intelligence lends support to the arguments that our own evolution of large brains and causal understanding were not precursors to our evolution of tool-use. The first hominid in the human lineage to unambiguously manufacture tools habitually was *H. habilis* (*c*. 2.5 Ma) whose hand resembled that of the modern human (Napier, 1962). This species also marked a considerable increase in brain size of 600-800 cm^3 from their contemporary australopithecines and extant African apes with 450-500 cm^3 (Pilbeam & Gould, 1974; Ambrose, 2001). Such large brains would have placed additional energy demands on the hominids, and tool-use was thought to grant them access to energy-rich foods such as termites, bone marrow, and the meat of thick-skinned animals (Ambrose, 2001). However, it wasn’t until the middle Paleolithic (*c*. 300 ka) that language and composite tool manufacture evolved (Lieberman, 1989; Kempler, 1992; Ambrose, 2001), suggesting some factor other than language and tool-use selected for large brains in *H. habilis*. A social intelligence ‘arms-race’ could perhaps offer a better explanation, with larger brains used to outwit, deceive, and co-operate with other individuals in a complex society (Whiten & Byrne, 1997).

The conditions in New Caledonia appear to have combined to select for tool-use in NC crows through a number of serendipitous means. The island’s geological and ecological history have culminated in habitats where the holes and crevices are filled with an un-tapped food resource, while the ancestors of NC crows were likely to possess inherited dispositions to insert sticks into holes combined with the necessary cognitive skills to use, select and modify innate objects as tools.

12.1 Appendix

```
> corvus<-aov(CorvusMaxBinoc~species)
> summary(corvus)
            Df Sum Sq Mean Sq F value    Pr(>F)
species      6 1110.4 185.060  19.311 1.618e-05 ***
Residuals   12  115.0   9.583
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
> TukeyHSD(corvus)
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = CorvusMaxBinoc ~ species)

$species
                                diff         lwr       upr     p adj
carrioncrow-americancrow  -4.4080405 -16.2766825  7.460601 0.8397908
jackdaw-americancrow       3.6848776  -8.8257695 16.195525 0.9365914
ncc-americancrow          19.4670861   6.9564390 31.977733 0.0020863 *
piedcrow-americancrow      4.2253621 -11.0969888 19.547713 0.9526219
raven-americancrow         1.1818986 -11.3287486 13.692546 0.9998437
rook-americancrow          4.6869456  -7.8237015 17.197593 0.8346936
jackdaw-carrioncrow        8.0929181   0.1804901 16.005346 0.0438074 *
ncc-carrioncrow           23.8751266  15.9626986 31.787555 0.0000031 *
piedcrow-carrioncrow       8.6334026  -3.2352393 20.502045 0.2250880
raven-carrioncrow          5.5899391  -2.3224889 13.502367 0.2500131
rook-carrioncrow           9.0949861   1.1825581 17.007414 0.0209457 *
ncc-jackdaw               15.7822085   6.9358451 24.628572 0.0006256 *
piedcrow-jackdaw           0.5404845 -11.9701626 13.051132 0.9999984
raven-jackdaw             -2.5029791 -11.3493425  6.343384 0.9468494
rook-jackdaw               1.0020680  -7.8442954  9.848431 0.9995560
piedcrow-ncc             -15.2417240 -27.7523711 -2.731077 0.0140340 *
raven-ncc                -18.2851875 -27.1315510 -9.438824 0.0001558 *
rook-ncc                 -14.7801405 -23.6265039 -5.933777 0.0011276 *
raven-piedcrow            -3.0434636 -15.5541107  9.467184 0.9735701
rook-piedcrow              0.4615835 -12.0490637 12.972231 0.9999994
rook-raven                 3.5050471  -5.3413164 12.351410 0.7989150
```

Table 5. Statistical output from an ANOVA model with post-hoc Tukey comparison. NC crows have a significantly larger binocular overlap than all other species. Two non-tool-using *Corvus* comparisons are significantly different: rooks and jackdaws both have a significantly larger binocular overlap than the carrion crow.

Order	Family	Species	Maximum binocular overlap(°)	Sources
Struthioniformes	Struthionidae	Common Ostrich *Struthio camelus*	20	G. R. Martin, G. Katzir, *Nature* **374**, 19 (1995).
Apterygiformes	Apterygidae	North Island Brown Kiwi *Apteryx mantelli*	11	G. R. Martin *et al., Plos One* **2**, (2007).
		Great Spotted Kiwi *Apteryx haastii*	11	"
Anseriformes	Anatidae	Northern Shoveler *Anas clypeata*	20	M. Guillemain, G. R. Martin, H. Fritz, *Functional Ecology* **16**, 522 (2002).
		Eurasian Wigeon *Anas penelope*	20	"
		Mallard *Anas platyrhynchos*	20	G. R. Martin, *Vision Res.* **26**, 1303 (1986).
		Blue Duck *Hymenolaimus malacorhynchos*	34	G. R. Martin, N. Jarrett, M. Williams, *Ibis* **149**, 112 (2007).
		Pink-eared Duck *Malacorhynchus membranaceus*	17	"
Sphenisciformes	Spheniscidae	King Penguin *Aptenodytes patagonicus*	29	G. R. Martin, *Ibis* **141**, 444 (1999).
		Humboldt penguin *Spheniscus humboldti*	45	G. R. Martin, S. R. Young, *Proc. Roy. Soc. B***223**, 197 (1984).
Procellariiformes	Diomedeidae	Grey headed albatross *Thalassarche chrysostoma*	27	G. R. Martin, *Proc. Roy. Soc.* B **265**, 665 (1998).
		Black-browed albatross *Thalassarche melanophris*	32	"
	Procellariidae	Antarctic Prion *Pachyptila desolata*	20	G. R. Martin, P. A. Prince, *Brain Behavior and Evolution* **57**, 33 (2001).
		White-chinned Petrel *Procellaria aequinoctialis*	40	"
		Manx Shearwater *Puffinus puffinus*	18	G. R. Martin, M. D. Brooke, *Brain Behavior and Evolution* **37**, 65 (1991).
Phoenicopteriformes	Phoenicopteridae	Lesser Flamingo *Phoeniconaias minor*	10	G. R. Martin, N. Jarrett, P. Tovey, C. R. White, *Naturwissenschaften* **92**, 351 (2005).
Ciconiiformes	Ciconiidae	White Stork *Ciconia ciconia*	28	G. R. Martin, J. M. Shaw, *Biological Conservation* **143**, 2695 (2010).
Pelecaniformes	Ardeidae	Squacco Heron *Ardeola ralloides*	20	G. R. Martin, G. Katzir, *Brain Behavior and Evolution* **44**, 74 (1994).
		Western Cattle Egret *Bubulcus ibis*	22	"
		Western Reef Heron *Egretta gularis*	20	"
		Black-crowned Night Heron *Nycticorax nycticorax*	22	G. Katzir, G. R. Martin, *Ibis* **140**, 157 (1998).
Suliformes	Phalacrocoracidae	Great Cormorant *Phalacrocorax carbo*	28	G. R. Martin, C.R. White, P.J. Butler Ibis 150, 39-48. 2008
Accipitriformes	Accipitridae	Short-toed snake eagle *Circaetus gallicus*	20	G. R. Martin, G. Katzir, Brain *Behavior and Evolution* **53**, 55 (1999).
Otidiformes	Otididae	Kori Bustard *Ardeotis kori*	21	G. R. Martin, J. M. Shaw, *Biological Conservation* **143**, 2695 (2010).
Gruiformes	Gruidae,	Blue Crane *Grus paradisea*	23	“
Charadriiformes	Burhinidae	Eurasian Stone-curlew *Burhinus oedicnemus*	18	G. R. Martin, G. Katzir, *Ibis* **136**, 448 (1994).
	Charadriidae	European Golden Plover *Pluvialis apricaria*	15	G. R. Martin, T. Piersma, *Proc. Roy. Soc. B* **276**, 437 (2009).
	Scolopacidae	Red Knot *Calidris canutus*	22	G. R. Martin, T. Piersma, *Proc. Roy. Soc. B* **276**, 437 (2009).
		Eurasian Woodcock *Scolopax rusticola*	12	G. R. Martin, *J.Comp.Physiol. A,***174**, 787 (1994).
	Laridae	Black Skimmer *Rynchops niger*	14	G. R. Martin, R. McNeil, L. M. Rojas, *Ibis* **149**, 750 (2007).
Columbiformes	Columbidae	Common Pigeon *Columba livia*	27	G. R. Martin, S. R. Young, *Vision Res*. **23**, 911 (1983).

		Mourning dove *Zenaida macroura*	11	B. F. Blackwell, E. Fernandez-Juricic, T. W. Seamans, T. Dolan, *Animal Behaviour* **77**, 673 (2009).
Psittaciformes	Psittacidae	Senegal Parrot *Poicephalus senegalus*	27	Z. D. Demery, J. Chappell, G. R. Martin, *Proc. R. Soc. B* doi:10.1098/rspb.2011.0374, (2011)
Strigiformes	Strigidae	Tawny Owl *Strix aluco*	48	G. R. Martin, *Vision Res.* **24**, 1739 (1984).
Caprimulgiformes	Steatornithidae	Oilbird *Steatornis caripensis*	38	G. R. Martin, L. M. Rojas, Y. M. R. Figueroa, R. McNeil, *Ornitologia Neotropical* **15**, 233 (2004).
	Caprimulgidae	Pauraque *Nyctidromus albicollis*	25	"
Bucerotiformes	Bucorvidae	Southern Ground Hornbill *Bucorvus leadbeateri*	30	G. R. Martin, H. C. Coetzee, *Ibis* **146**, 18 (2004).
		Southern Yellow-billed Hornbill *Tockus leucomelas*	30	"
Passeriformes	Tyrannidae	Black Phoebe *Sayornis nigricans*	40	M. D. Gall, E. Fernandez-Juricic, J.Comp.Physiol. A, **196**, 15 (2010).
	Corvidae	California Scrub Jay *Aphelocoma californica*	35	E. Fernandez-Juricic, C. O'Rourke, *J. Comp. Physiol. A* **196,** 879 (2010).
		American Crow *Corvus brachyrhynchos*	42	"
		Eurasian Magpie *Pica pica*	45	(this study)
	Sturnidae	Common Starling *Sturnus vulgaris*	43	G. R. Martin, *J.Comp. Physiol. A,* **159**, 545 (1986).
	Passeridae	House Sparrow *Passer domesticus*	46	E. Fernandez-Juricic, M. D. Gall, T. Dolan, V. Tisdale, G. R. Martin, *Ibis* **150**, 779 (2008).
	Fringillidae	House Finch *Carpodacus mexicanus*	46	E. Fernandez-Juricic, M. D. Gall, T. Dolan, V. Tisdale, G. R. Martin, *Ibis* **150**, 779 (2008).
	Icteridae	Brown-headed cowbird *Molothrus ater*	51	B. F. Blackwell, E. Fernandez-Juricic, T. W. Seamans, T. Dolan, *Animal Behaviour* **77**, 673 (2009).

Table 6. Maximum binocular overlap in birds. Data were compiled in the course of an exhaustive literature review. Taxonomy and species names follow the International Ornithological Congress World Bird List (Gill & Wright, 2006). The species names used here may not be the same as those used in the sources cited.

```
> t.test(PasserineMaxBinoc~taxa, alternative='two.sided', conf.level=.95,
+   var.equal=FALSE, data=Dataset)

        Welch Two Sample t-test

data:  PasserineMaxBinoc by taxa
t = 9.158, df = 6.182, p-value = 8.025e-05
alternative hypothesis: true difference in means is not equal to 0
95 percent confidence interval:
 13.04314 22.46246
sample estimates:
      mean in group ncc mean in group passerine
               61.46709                43.71429
```

Table 7. Statistical output from a Welch two-sample t-test using unequal variance, showing NC crow maximum binocular overlap is significantly larger than all other passerine species for which data are available (see appendix Table 6).

```
Welch Two Sample t-test

data:  logOtherMaxBinoc by taxa
t = 16.2608, df = 37.271, p-value < 2.2e-16
alternative hypothesis: true difference in means is not equal to 0
95 percent confidence interval:
 0.3922415 0.5038758
sample estimates:
         mean in group ncc mean in group nonpasserine
                  1.788636                   1.340577
```

Table 8. Statistical output from a Welch two-sample t-test using unequal variance, showing NC crow maximum binocular overlap is significantly larger than all other non-passerine species for which data are available (see appendix Table 6).

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