Development of tool use in New Caledonian crows: inherited action patterns and social influences

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ABSTRACT

New Caledonian crows (*Corvus moneduloides*) are the most advanced avian tool makers and tool users. We previously reported that captive-bred isolated New Caledonian crows spontaneously use twig tools and cut tools out of *Pandanus* spp. tree leaves (an activity possibly under cultural influence in the wild). However, what exactly is inherited and how it interacts with individual and social experience remained unknown. To examine the interaction between inherited traits, individual learning, and social transmission, we observed in detail the ontogeny of twig tool use in hand-reared juveniles. Successful food retrieval was preceded by stereotyped object manipulation action patterns that resemble components of the mature behaviour, demonstrating that tool-oriented behaviours in this species are an evolved specialisation. However, there was also an effect of social learning: juveniles which had received demonstrations of twig tool use by their human foster parent showed higher levels of handling and insertion of twigs than their naïve counterparts; and a choice experiment showed that they preferred to handle objects which they had seen being manipulated by their human foster parent. Our observations are consistent with the view that individual learning, cultural transmission, and creative problem solving all play roles in the acquisition of the tool-oriented behaviours in the wild, but demonstrate a greater role for inherited species typical action patterns than was heretofore recognised.

INTRODUCTION

New Caledonian crows (*Corvus moneduloides*, hereafter ‘NC crows’) are renowned for their complex tool-oriented behaviour (hereafter ‘TOB’), which involves both tool use and manufacture. In comparison with most other tool-using animals (see Beck 1980; Kacelnik et al. in press), this species stands out with regard to: the frequency of their TOB and the diversity and complexity of tool shapes routinely used in the wild (Hunt 1996; Hunt 2000; Hunt & Gray 2002; Hunt & Gray 2004a; Hunt & Gray 2004b); their ability to select tools appropriate for a given task (Chappell & Kacelnik 2002; Chappell & Kacelnik 2004); and their capacity to create novel tools according to need (Weir et al. 2002). Furthermore, circumstantial evidence in the form of regional variation suggests cultural transmission may be involved in tool manufacture (Hunt & Gray 2003). This suite of attributes makes the species particularly interesting as a research model for studying the acquisition of TOB, but till now a detailed study of the process has been lacking. Some of the theoretical questions are similar to, and also relevant to, problems posed by acquisition of TOB in all other species, including humans.

The emergence of tool use in the human child involves a complex interplay between inherited, individually learnt, and social factors. It therefore presents a challenge to experimental studies, not least because many developmental experiments, such as long term manipulation of the social or physical environment, cannot be performed. Birds, however, are particularly suitable for this type of study, both because of the possibility of experimentation and because their rapid development makes practical experiments which would be much more time consuming to conduct in primates. With care, insights gained from such studies may allow parallels to be drawn that could promote understanding of general principles of behavioural development, including the evolution and individual development of TOB in our own species.

We hand-raised four captive-bred NC crow chicks under controlled laboratory conditions to investigate the role of both social and non-social factors in the ontogeny of TOB in this species. Two crows received regular demonstrations by their human foster parent of how to use twig tools for retrieving food, whereas the other two birds never saw tool use. We have reported elsewhere (Kenward et al. 2005) that all four juveniles spontaneously began to use twig tools to obtain otherwise inaccessible food at similar ages, and that one untutored subject promptly manufactured functional tools when exposed to pandanus (*Pandanus* spp.) leaves. The remaining birds showed interest in the leaves but within the short time during which we had fresh leaves available were not observed to use them to make tools. These findings demonstrated conclusively that the species possesses an inherited predisposition for using and manufacturing tools. In this paper, we present detailed ethological data and further analyse the development of TOB in these individuals, in order to examine how inheritance and experience interact during development and to examine the influence of social inputs. To achieve these goals, we: (i) describe in detail the development of TOB so as to determine more precisely what is inherited; and (ii) investigate whether demonstrations of tool use by human foster parents have a measurable effect on the ontogeny of TOB.

Tool use does not necessarily require a high level of cognition (e.g. Hansell 2000). For example, there is no reason to believe that the sensorimotor integration required for, say, carrying eggs to safety on a leaf by a fish (Timms & Keenleyside 1975) is any more cognitively demanding than the foraging and courtship behaviours which allowed the fish to produce the eggs. However, TOB may be particularly revealing about processes of physical cognition, because it involves creating relationships between two or more external objects in a manner which is easily observable (and amenable to experimental manipulation). Our finding of an inherited predisposition for TOB in NC crows (Kenward et al. 2005) raises the questions of exactly what is inherited.

Many hypotheses are conceivable, varying in how the canalization (sensu Waddington 1957) is achieved (and therefore also how robust it is). Rigid developmental programs for sets of motor patterns could be under tight genetic control, with little variation in adult behaviour being explained by the subject’s experience. Other hypotheses, however, allow for varying degrees of learning. Animals could inherit a general tendency to explore objects in a manipulatory fashion, leading to the acquisition of various modalities of tool use by reinforcement of random or exploratory object-manipulation acts. Alternatively, each juvenile NC crow could be equipped with cognitive mechanisms which allow it to learn physical laws by observing object interactions, and then plan goal-directed TOB exploiting these laws (a process customarily identified as 'insight', see Thorpe 1963). The concept itself is problematic, and even ignoring the conceptual difficulties, evidence of insight in non-human animals is rare and controversial. We use the term, however, for its heuristic value and because it can be separated from other extreme alternatives by specific predictions about the acquisition of behaviour.

Each of these hypotheses predicts different observable patterns of behaviour development. Insight would result in sudden marked changes in behaviour, with immediate drop-off of inefficient behaviours following the moment when the bird mentally solves each problem. If motor patterns are under tight genetic control, then one might expect to see incomplete actions emerging prior to the directly functional versions (similar to the rehearsal of flight movements by chicks before fledging), and less individual variation would be observed than under the hypotheses involving looser canalization. If TOB emerges because of a general manipulatory tendency coupled with learning, the predictions depend upon the type of learning. If operant conditioning was responsible, specific tool-related acts would begin to dominate the repertoire of object oriented behaviour only after they had been associated with food rewards. However, an alternative form of learning, perception-action development (e.g. Gibson & Pick 2000), does not require food reinforcement. If discovery itself is reinforcing, then this account would also explain the motivation to explore. This hypothesis predicts that individuals would persistently perform actions which enable them to learn more about the affordances of objects and the environment.

These hypotheses are not necessarily mutually exclusive – different processes may be involved at different developmental stages and besides, different levels of cognition could accompany the performance of externally similar actions. For example, it is unlikely that insight precedes or causes the early stages of the acquisition of tool use in children (Lockman 2000), but it is obviously available to older individuals. Moreover, an individual is unlikely to experience insight regarding tool use unless it possesses tendencies which already caused it to experience the manipulation of objects, so a sudden transition might not be present in overt behaviour even if it does occur in underlying cognitive processes.

Distinguishing between inherited motor patterns and a general manipulatory tendency is also problematic. Inherited motor patterns may be accompanied by learning – even a spider building its web according to a rigid set of inherited motor patterns is able to use experience to modify its web so as to take maximum advantage of the available prey (Heiling & Herberstein 1999). Conversely, lack of observable evidence for inherited motor patterns does not rule them out. For these reasons, our goal is not to categorise TOB in NC crows as being the result of one particular process (for instance, deciding whether TOB is cultural or not) but to determine as precisely as possible how the complex behaviour of adult NC crows emerges from the interaction of heritable trends and specific individual and social learning processes (see Bateson 1978; Bateson 1991 for discussions of this general approach to understanding development of behaviour).

In the only other study of the ontogeny of twig tool use in birds, the presence or absence of adult demonstrators made no significant difference to the time it took juvenile woodpecker finches (*Cactospiza pallida*) to start using tools successfully (Tebbich et al. 2001). Two other TOBs have been observed to develop in isolated birds – egg breaking with stones by Egyptian vultures (*Neophron percnopterus*) (Thouless et al. 1989), and the use of pieces of plant material to wedge nuts while opening them by hyacinth macaws (*Anodorhynchus hyacinthinus*) (Borsari & Ottoni 2005) – thus proving that social input was not necessary. For wild NC crows, however, there is circumstantial evidence suggesting that birds acquire at least certain tool manufacture skills by social learning: crows cut tools from the edges of the rigid, thorny leaves of pandanus trees, with tool shapes varying regionally in shape and complexity in a manner consistent with cultural transmission (Hunt & Gray 2003). The possibility that aspects of TOB are culturally sustained would be strengthened if we could show that social influence indeed plays a role in NC crow development of TOB. If social factors are important, one should expect not only long term regional differences in the shape of tools produced by adults but also short term influences on manipulatory behaviour according to the exposure to tutors. We therefore also conducted an experiment with our tutored birds to investigate if NC crows match object choice to that of a human demonstrator.

In summary, although we do not see TOB as necessarily demanding in cognitive terms, we see it as a revealing behaviour that allows for a general understanding of animal physical cognition and in particular its development. For this reason, as far as possible we place the developmental observations of TOB in the general framework of behavioural development in birds.

METHODS

Subjects and Housing

The subjects were four laboratory-born, hand-reared NC crows. They comprised two male siblings named ‘Oiseau’ and ‘Corbeau’, a male named ‘Nalik’ and a female named ‘Uék’ (all words meaning crow or bird in languages spoken in New Caledonia). All were offspring of members of our colony, and one (Uék) was the daughter of an individual (Betty) who has participated in all previous studies with captive NC crows in our laboratory. This was the first successful breeding of NC crows in captivity, and we used all available subjects. Uék was incubated by her parents and removed from the nest at 1 day old. The other subjects came from eggs that were removed from the nests shortly after being laid and artificially incubated. The chicks were hand-raised in artificial nests, initially in brooders and then in small pens mounted at table level in indoor aviaries. Pens were left open during the day, allowing the chicks to leave them at fledging. As nestlings, the birds showed a gradually increasing tendency to locomote inside and then outside the nest, so there was no sharp fledging point. At 25-26 days old, however, all four birds began to leave the nest and climb around the perches – a behaviour known as branching. We took branching, rather than fledging, as the starting point for recording behaviour, because it was at this stage that they began to locomote and manipulate objects.

Each aviary measured 3.3 by 3.9 by 2.5 m high, was on a natural daylight cycle, contained natural wooden perches and a woodchip substrate, and was enriched with at least 30 twigs of assorted shapes and sizes, live vegetation, ropes, toys and mineral blocks (some suspended from perches and some unattached). Holes, drilled into perches and into logs on the floor, were regularly provisioned with chopped meat and mealworms, most of which were accessible only through tool use.

Additional holes and crevices were used for tool use demonstration (see below), though they were also regularly replenished with food outside of experimental sessions. Five wooden blocks, with holes drilled horizontally 2 cm wide and 7 cm deep, were mounted onto perches, each in a different position in the aviary (the block holes; Fig 1a). Five crevices, of length 7 to 11 cm, depth 2 to 6 cm, and width 4 to 18 mm, were made with pairs of parallel wooden plates, and mounted on a wooden platform fixed to the wall (the crevice platform; Fig 1b). Crevice platforms were not installed in the aviaries until mid-way through the observation period (see below).

FIGURE 1 ABOUT HERE

Growing nestlings were hand-fed chopped neonate rats (supplied frozen by Livefoods Direct®) with vitamin supplements; the amounts of this food type provided through active feeding were reduced gradually as the birds weaned. Post-fledging, the subjects had ad libitum access to the food mixture that we use to feed adult crows in our captive colony (soaked Go-Cat® cat biscuits, Orlux Universal® and Orlux Granules® insect and fruit mixes, peanuts, and mealworms). However, the most preferred food, meat, was only available during hand-feeding, by tool use, and during experimental and observation sessions (see below). Drinking and bathing water were permanently available. Each bird also had a cage (90 by 60 by 80 cm high) inside the home aviary, into which it was placed at night and also sometimes during experimental sessions (see below).

To determine the effects of demonstration of tool use by human foster parents while allowing them to experience social contact with a conspecific, we tried to keep the birds as two pairs, – the tutored group (Uék and Nalik), and the untutored group (Oiseau and Corbeau) – each in its own aviary. However, midway through the experiment, 33 and 34 days post-branching, Oiseau and Corbeau started to show a level of mutual aggression that potentially threatened their welfare, and they were therefore separated before they had a chance to injure one another. Thereafter one of them (rotated during the study) was housed in a separate covered outdoor aviary, of similar size as the other aviaries, and provisioned and enriched in the same way as described above.

Ethical Note

Although no individuals were originally intended to be housed alone, due to the split of the untutored group, this became inevitable. However, because the individuals were hand-raised, they had frequent human social contact, not only during experimental sessions but also during additional informal ‘play’ sessions.

Treatment and Observation Procedure

We first observed informally what type of behaviours the juveniles exhibited. On the basis of these preliminary observations, we defined behaviours for subsequent use in formal ethogram recording. Uék was the oldest, and she was therefore observed for this purpose until she was 21 days post-branching (at which time Nalik was 7, Corbeau 1, and Oiseau 0 days post-branching), when regular formal experimental observation sessions began. As the ethogram forms an integral and original part of this study, we report detailed descriptions and definitions of behaviours in the Results section.

There were three types of session: ‘observation’ sessions, which were for all birds, and two experimental session types – ‘teaching’ sessions, only for the tutored group, and ‘control’ sessions, for both groups. Before an observation session started the target individual and the co-housed bird were both placed in their cages, which were then covered so that the birds were unable to observe the experimenter (always BK) manipulate objects in the aviary. Food was removed from the aviaries, and meat was replenished in each of the five block holes. To give the subject easy access to suitable tools, ten twigs were taken from the floor and five each placed on two small perch-mounted platforms. The target bird was then released from its cage (the other bird remained within its covered cage throughout the session), and the experimenter sat on a chair in the aviary and observed the bird for 30 minutes, using a custom-written event recorder on a standard laptop. During 10% of the sessions a second experimenter was present, to make simultaneous video recordings for documentation purposes. Behaviour oriented towards the experimenters was infrequent in comparison to other behaviour types until the later stages of observation (see below), and was discouraged whenever it occurred by gently displacing the bird away from the experimenter.

Teaching sessions were as observation sessions, except for the addition of demonstrations by the human experimenter. There were five demonstrations during each teaching session, at the start and at 6 minute intervals thereafter. For each demonstration the experimenter got up from his chair, picked up a twig from the floor, used it to retrieve a piece of meat from one of the block holes, and left the meat for the bird to eat (the twig was also left in the hole; see supplementary movie clip 1 in Kenward et al. 2005). When the birds ranged between 25 and 49 days post-branching, two modifications were made to this protocol: firstly, on two randomly selected demonstrations per session, the food was withheld in order to encourage the birds to obtain food for themselves, similarly to what has been reported in birds of other species feeding nestlings (Davies 1976); and secondly, two random demonstrations per session took place at a crevice on the crevice platform instead of at a block hole. The decision to include crevices was based on the observation that early tool manipulations were rather clumsy. To increase the chance of emergent TOB resulting in food rewards we therefore presented a food retrieval task which was still naturalistic but easier than the block holes because they required a less delicate manipulation of the tool.

Control sessions were as teaching sessions except that, instead of retrieving meat from the hole with a twig, a new piece of meat was placed next to the hole at the appropriate times. To control for the amount of local enhancement at the meat delivery sites across session types, the time taken to produce meat was the same in teaching and control sessions. Subjects in the untutored group were never exposed to tool use for food retrieval, or handling of twigs or twig-like objects (such as pens); due to experimenter error, however, Oiseau was exposed to twigs being picked up and placed on the platforms on four brief occasions between 33 and 37 days post-branching, but, like Corbeau, never witnessed tool use.

NC crows in the field continue to receive parental feeding for many months after fledging (Kenward et al. 2004), and we therefore continued to offer food to the subjects by hand at 1.5 hour intervals throughout the observation period. Feedings were staggered so that roughly half the sessions took place immediately after feeding, with the other half taking place approximately 45 minutes afterwards.

The criterion for termination of the formal observation and demonstration period was when the bird had reached the stage of successful tool use, defined here as the successful retrieval of food from either a hole or a crevice. In 3 birds, however, human-oriented behaviours increased to such a level that data recording was terminated prematurely to avoid biased data. In these cases, informal observation from outside the aviary and remote video recording were continued solely for the purpose of confirming successful tool use. Formal observation and demonstration lasted until 51 days post-branching for Uék, 38 for Nalik, 43 for Corbeau, and 44 for Oiseau.

Sessions took place between 07h30 and 19h30, were blocked pseudo-randomly so that different types occurred at all times throughout the day, and the different types were spread evenly throughout the period. Prior to 8 days post-branching, however, there were only observation sessions (i.e. neither teaching nor control sessions), because the birds were not yet mobile enough to follow and observe the demonstrator. Due to logistic constraints, it was impossible to employ a fully balanced design over the entire observation period (most noticeably, no data exists for Nalik in week 7), but the mean numbers of sessions per day were similar for the tutored and untutored group (tutored group: 0.5 observation sessions / day, 1.2 teaching sessions / day, and 0.3 control sessions / day; untutored group: 0.6 observation sessions / day, and 1.1 control sessions / day).

We also tested the crows' response to leaves from trees of the genus *Pandanus*, similar to those from which wild individuals make tools that vary regionally in shape and complexity; we do not give details here because these experiments have been presented elsewhere (Kenward et al. 2005).

Statistical Analysis

As measures of the birds' behaviour, we calculated the proportion of time spent performing certain acts in each observation session. For parametric statistical analyses, we used arcsine square root-transformation of response variables to normalise errors (Zar 1999). We employed general linear models (GLM), using sequential sums of squares (Grafen & Hails 2002). We checked model fit by inspecting diagnostic scatter plots, using standardised residuals (Grafen & Hails 2002). All models were implemented in Minitab 14.1. 'Treatment group' was included as a factor in some of our GLMs. Because of the limited sample size, results of those analyses cannot be generalised beyond the four subjects investigated, and we consider the robustness of this aspect of our study in the Discussion.

Analyses of proportional data, as carried out in this study, may suffer from the 'unit sum constraint': as the proportion of one behaviour increases, the proportions of other behaviours are bound to decrease. Our analyses, however, were unlikely to be affected by this problem, as the behaviours of interest were performed infrequently and proportions were therefore comparatively small (see Results, especially Fig. 6). It is worth reporting that we also modelled our data with continuous time Markov chains, which overcome problems of non-independence inherent in proportional data (Haccou & Meelis 1992); all analyses, however, yielded similar results to with the proportional data, and we therefore present proportion results only, because of their more intuitive interpretation.

Matching of Object Choice

To further examine the importance of social input, we conducted an experiment into object choice with the two tutored subjects, when they were between three and four months post-branching (two months after formal observation and demonstration ended). We used thirty-two novel objects, mainly small toys and household items, that were small enough for an NC crow to carry. We assigned objects into 16 pairs so that each object in a pair would be of roughly similar attractiveness; we based this matching on criteria such as size and shininess.

A random object from each pair was assigned as the target object for Uék, and the other object for Nalik. Each object pair was then tested with each bird over 32 trials as follows: both birds were placed in their cages, which were covered with an opaque material, and then the objects were placed 40 cm apart on a table in the aviary, and also covered with an opaque material. The location of the target object was pseudo-randomised so that it could not occur on the same side for more than two trials in a row for one individual, and so that the target object was on each side eight times for each bird. The subject was then released from its cage, and a minute later the experimenter removed the object's cover and began the session, which consisted of a one minute demonstration period and a subsequent three minute period with no demonstration, followed by an additional demonstration and a non-demonstration period (so the sequence was Demo 1; Non-demo 1; Demo 2; Non-demo 2).

During the demonstration periods, the experimenter manipulated the target object by lifting it from the table and slowly rotating it in one hand, replacing it at the end. During the non-demonstration periods, the experimenter sat still on a chair. The bird had free access to both objects at all times – the experimenter allowed touching of the target object during demonstration but did not allow it to be carried away. If the objects had been moved by the bird in the first half of the session they were replaced in position before the second manipulation period, using a cover over the non-target object to prevent the subject seeing it manipulated. The sessions were video recorded and subsequently scored to determine, for each period, which object was manipulated most often, and for which object a bout of manipulation began first.

RESULTS

General Pattern of Development and Ethogram Definitions

All four birds followed a qualitatively similar developmental pattern. We therefore begin by describing this common pattern, and providing definitions to be used in the ethogram (Table 1). We define three classes of object manipulation, namely: four kinds of 'touching' (including 'carrying'); four kinds of 'precursor actions', so named because they resemble aspects of mature tool use but are not directly functional in terms of allowing access to food; and actions of 'insertion', which we treat as directly functional because they can result in successful food extraction, and/or possibly food caching. Precursor actions were first observed in the second week post-branching, and reached a maximum level in week 4, at the same time that the first insertion actions occurred; the frequency of precursor actions remained roughly constant thereafter, whereas insertions increased steadily over the remaining observation period (Fig. 2). Of the four precursor behaviours, the most common were 'rubbing' and 'proto-probing' (Table 1, Fig. 3, Supplementary videos 1 and 2, respectively). Proto-probing was a particularly striking behaviour in which the birds held twigs in their beaks and moved them back and forth, in a similar manner to how they probe holes and crevices, except that the twig was not inserted in any hole or crevice.

TABLE 1 ABOUT HERE

FIGURES 2 AND 3 ABOUT HERE

‘Touching’ starts while locomotion is only just beginning to develop, and ‘carrying’ develops in step with locomotion (Fig. 4). The objects manipulated changed as the birds developed (Fig. 5). As for caching, we observed that food was often inserted into holes and left there. The crows usually, but not always, retrieved the food immediately. This behaviour appears to be proto-caching, but unfortunately we were unable to collect data on whether individuals specifically retrieved food they had hidden.

FIGURES 4 AND 5 ABOUT HERE

Comparison of Treatment Groups

First we examined whether the behaviour of the two subjects in the tutored group differed significantly between teaching, observation, and control sessions. Taking only the data for Nalik and Uék, we formulated GLMs, entering in the following order these predictor terms: ‘age’ (in days since branching began) as a covariate, ‘individual’, and ‘session type’ as fixed factors, and the four possible interactions terms. Of seven response variables, session type and its interactions were not significant predictors for the following six: locomotion, twig carrying, non-food non-twig item carrying (e.g. toys or wood chips), food inserting, non-food non-twig item inserting, or twig inserting. The only variable which session type significantly affected was food carrying ($F_{1,114} = 10.18$, $P < 0.001$), with birds showing a higher proportion of this behaviour in teaching and control sessions compared to observation sessions; this is somewhat trivial, as food was not provisioned in observation sessions (see Methods).

For the six variables statistically unaffected by session type, we pooled data from the different sessions to compare behaviour between treatment groups. To examine the effect of social experience we fitted GLMs, entering in the following order these predictor terms: ‘age’ as a covariate, ‘individual’ nested within ‘treatment group’ and ‘treatment group’ as fixed factors, and the interactions between ‘age’ and ‘individual’, and between ‘age’ and ‘treatment group’ (Table 2).

FIGURE 6 AND TABLE 2 ABOUT HERE

As might be expected, the frequency of all analysed behaviours increased with age (Fig. 6). More important, however, is that we found significant positive effects of tutoring on the proportions of twig carrying (Fig. 6a) and twig inserting (Fig. 6b). For twig carrying, and all types of inserting, there were significant interactions between treatment group and age, indicating that the tutored group had a faster rate of increase in the frequency of those activities (Fig. 6a,b,d,e). For locomotion and non-food non-twig item carrying, we found individual differences but no significant differences between treatment groups (Fig. 6c,f).

Matching of Object Choice

Both birds were eager to manipulate the objects, during both the demonstration and non-demonstration periods – in only two trials out of 32 did a bird not manipulate both objects at least once. Nalik performed a mean ± SE of 11.4 ± 1.1 bouts of touching per trial with mean length of 10.1 ± 0.8 s, and a mean of 5.0 ± 0.9 carrying bouts with mean length of 8.6 ± 1.5 s – corresponding figures for Uék were, respectively, 11.2 ± 0.7 bouts and 10.7 ± 0.8 s; and 8.6 ± 0.9 bouts and 7.7 ± 0.7 s. On six occasions a bird picked up one object and poked the other object with it.

The birds demonstrated a clear preference for the target object (Fig. 7), both in terms of which object they manipulated first, and which object they manipulated most often. There was a trend for this effect to increase in the second half of the trial, so that the target object was not manipulated significantly more often until the demonstration 2 period.

FIGURE 7 ABOUT HERE

DISCUSSION

General Pattern of Development

In all detailed studies of the ontogeny of avian object oriented behaviour of which we are aware, similar patterns of development have been observed: precursor behaviours (with no direct function) appear first, with directly functional behaviours emerging in the course of gradual improvement. The following are some examples. In song thrushes (*Turdus philomelos*), snail-smashing on anvils is preceded by the attempted smashing of non-snail objects, and also by flicking movements in which the object does not connect with the anvil (Henty 1986). In laughing gulls (*Larus atricilla*), the pecking response at the parent's bill which elicits parental feeding is initially sometimes directed at inappropriate objects, and improves in accuracy over time (Hailman 1967). Even in precocial species, such as the greater rhea (*Rhea americana*), feeding motor patterns are initially displayed when there is no relevant stimulus (Beaver 1978). Caching Parids begin by inserting food items into crevices without actually letting go and leaving them in place (Clayton 1992; Haftorn 1992). In the development of tool use in woodpecker finches (*Cactospiza pallida*), juveniles pass through a number of tool-oriented developmental stages before successfully using tools, such as ‘uncoordinated manipulations’ and ‘exaggerated, playful movements’ while holding twigs (Tebbich et al. 2001).

Nest building is particularly relevant to our study because it also involves twig handling. Its ontogeny, however, has hardly been studied, with a notable exception provided by Collias and Collias (1964; 1973; 1984) who report that village weaverbirds (*Textor cucullatus*) begin manipulating nest materials within weeks of fledging and continue to do so until they build their first nest. Kortland (1955) describes how cormorant chicks (*Phalacrocorax carbo*), still in the nest, perform a quivering movement with the head while holding a twig, a movement they later combine with a jab which incorporates the twig into the nest. Many non-object oriented avian behaviours also develop in a similar manner, such as dust-bathing (Larsen et al. 2000) and social display (Groothuis 1993).

In addition to the presence of precursors, the TOB we observed in NC crows has other things in common with all these avian behaviours. Although developmental field work is missing, the fact that all four individuals developed tool use in a qualitatively similar manner implies that the TOBs we observed in these juveniles are species-typical and include stereotyped action patterns such as proto-probing which develop in a predictable manner without the need of being shaped by successful food extractions. Similarly to other cases of an apparently missing role for food reinforcement, such as song learning or imprinting, experience may still have a role in shaping the functional behaviour, because the sensory feedback from rubbing twigs against any substrate may serve to hone the motor control to be used later on in food extractions.

The involvement of stereotyped, inherited action patterns would once have earned TOB the description of ‘innate’. Due to many problems with the term, however, including that it discourages investigation of development without actually explaining it (Lehrman 1953; but see Lorenz 1965; Berridge 1994; Marler 2004), and that it has been variously defined as implying a number of different characteristics which have not in fact been shown to reliably co-occur (Mameli & Bateson, in press), the term has been almost abandoned. We prefer to avoid the label, partly for these reasons, but also because of its common but unwarranted association with non-intelligent behaviour. It has often been assumed that there is a trade off between the degree of inheritance of patterns of behaviour and their cognitive sophistication: behaviour seen to be largely innate (or instinctive) is in these cases assumed to be less likely to be accompanied by complex cognition. In fact, a rich hereditary endowment (such as the human predisposition for language acquisition, the inclination to social nesting in parrots or the use of tools in NC crows) may be the platform that allows and enhances sophisticated cognitive development (see Gibson 1990). In the case of TOB, we have found that NC crows do have an inherited developmental program that includes well defined motor schemes, some of which emerge before their integration in directly functional TOB. This does not exclude the intervention of flexible cognitive processes in the acquisition and/or deployment of the behaviour.

It has been argued (Hansell 2000) that because nest building rivals NC crows' TOB with respect to diversity of materials used and complexity of their combination, TOB may not be cognitively more complex, and may be under tight genetic control, as nest building seems to be. As we have argued, however, the presence of inherited action patterns does not exclude advanced cognition, and indeed from this perspective nest building may have been underestimated in its cognitive sophistication, rather than TOB being overrated.

The inherited component we observed in the development of TOB opens the possibility that regional differences in tool manufacturing, especially those shown for tools made with pandanus leaves (Hunt & Gray 2003) could be due to genetic differences. This possibility requires some attention before conclusions about cultural transmission are accepted, especially given that it is known that complex sequences of action patterns can be inherited (e.g. Colonnese et al. 1996), and the recent discovery that spatial genetic variation can be maintained over surprisingly small scales (Garant et al. 2005).

We have suggested that a possible function of the precursor behaviours is to hone the functional TOB. However, behaviour performed by juveniles which resembles that of adults without achieving the same ends need not be causally related to the emergence of adult behaviour, but instead may be expressed as a consequence of maturation of the organism's nervous system (Harrison 1904; Haverkamp & Oppenheim 1986). Amongst the previously mentioned avian behaviours, there are several examples where denying juveniles the chance to perform precursor behaviour does not prevent them from later performing the directly functional behaviour. This is true for nest-building (Collias & Collias 1973); feeding in chicks (Cruze 1935; Hailman 1967); caching in Parids (Clayton 1994); and snail-breaking by thrushes (Henty 1986). Similarly, one of our subjects made functional tools on the first day of being exposed to pandanus leaves (Kenward et al. 2005). Experimental manipulation can even cause precursor behaviours to be replaced earlier by the directly functional behaviour – gull chicks, which perform precursor versions of aggressive social displays, can be caused by testosterone administration to perform the full display (Groothuis 1989; Baerends 1990). The "precursor" label is thus just descriptive, and the function of such behavioural patterns must be seen as a topic to investigate, rather than assuming that they serve to prepare the adult's version of the behaviour.

It is likely, however, that the precursor behaviours do serve some function. Hogan (1994; 2001) has argued that in the development of behaviour "systems" ranging from hunger and feeding to social displays, some general principles apply. In his view, motor, perceptual, and central control mechanisms pertaining to different systems often initially develop independently, but later become integrated. For example, motor components of dustbathing in fowl are at first performed in the absence of any eliciting stimuli, and only later become connected to the perceptual and control mechanisms (Kruijt 1964). NC crow TOB can fit this idea. The motor mechanisms which will later result in hole-probing are initially performed in the absence of the stimulus provided by holes, resulting in proto-probing. Later, the same motor mechanisms become integrated with perceptual and control mechanisms which allow the behaviours to be performed at the appropriate times.

In junglefowl chicks (*Gallus gallus spadeus*) hunger and pecking are under independent control immediately after hatching, and chicks must learn that pecking leads to ingestion before the systems can function together (Hogan 1984). The initial function (or at least the consequence) of pecking is thus not primarily to allow the chick to feed, but rather to allow learning about the consequences of pecking. Similarly, the function of the NC crow precursor behaviours might be to learn about the consequences of object manipulation. Clearly, they cannot learn how to extract food from proto-probing. But, just as the junglefowl chicks need to learn about ingestion before they can learn what to eat, the crows may need to learn fundamentals such as that inserting into a solid object is only possible at a concavity.

This form of tool use acquisition, in which the affordances of objects and surfaces are learned by trial and error manipulation beginning at an early stage of development, has also been described as perception-action development, and has been argued to be of fundamental importance in the acquisition of tool-oriented skills in children and other primates (Gibson & Pick 2000; Lockman 2000). Although couched in different language, this interpretation is consistent with classic explanations for behaviour development – for example the way in which begging gull chicks are born with a tendency to peck at objects resembling their parent's beak, but subsequently learn more about the relevant stimuli and the results of their own actions (Hailman 1967).

Confirming the importance of perception-action routines for NC crows requires additional experiments, but the idea provides a good framework to think about, for example, the emergence of insertion out of proto-probing. Note that this account assumes some form of internal reinforcement for inserting objects, which would itself need to be inherited, because the subjects performed many insertions over a period of several weeks before they resulted in food rewards. Object insertion could be inherently rewarding, and/or the learning of affordances enabled by the act could be rewarding. The latter possibility is emphasised by traditional accounts of perception-action learning, but the fact that the crows persisted in performing actions without food reward long after they had probably learned their consequences means the former is also a likely factor. A similar process could also explain the occurrence of precursor action patterns – it may be that what are inherited are not developmental programs for motor patterns, but rather for tendencies to find certain actions rewarding.

Perception-action learning may also be important in the acquisition of more sophisticated forms of goal-directed control, for example learning the relationship between holes of certain depths and diameters and twigs of appropriate dimensions, which leads to the known ability of adults to select and modify tools for specific circumstances (Chappell & Kacelnik 2002; Weir et al. 2002; Chappell & Kacelnik 2004). Indeed, it is reasonable to speculate that natural selection may act on variance for what constitutes reinforcement, and that minor mutations in this may lead to the emergence, by the normal, pre-existing processes of learning by reinforcement, of vastly different adult behaviour. The process of discovering internally reinforced actions by exploring possible behaviours would manifest as play.

Much of the crows' object-oriented behaviour can be described as play, which is frequently observed in birds (Ficken 1977; Ortega & Bekoff 1987; Diamond & Bond 2003). Burghardt (2005) defines play as “repeated, incompletely functional behaviour differing from more serious versions structurally, contextually, or ontogenetically, and initiated voluntarily when the animal is in a relaxed or low-stress setting”. In our subjects, precursor behaviours continued after directly functional behaviour had been developed; indeed, our wild-caught adults also frequently show apparently functionless behaviour, such as inserting stones into holes in logs and repeatedly breaking pieces of wood. As a prolonged development period, including much play, is thought to be an adaptation that allows animals to develop a variety of skills (e.g. Burghardt 2005), the play observed in NC crows could enable them to learn the wide range of TOBs displayed by the species in natural circumstances. Our subjects sometimes engaged in playful behaviours which did not fit easily into our ethogram categories and consequently were not recorded formally in detail: for example, Oiseau sometimes spent time holding one end of a long cardboard tube whilst running on the ground pushing the tube along in front. These observations supports the hypothesis that behaviour which allows the learning of object affordances is inherently rewarding.

Caching

Our observations of food being frequently inserted and left in holes supports the hypothesis that NC crows are a caching species, although we did not record whether the birds retrieved food after a long enough period for this to be conclusive. Inserting and quickly retrieving food is a precursor to caching in titmice (*Parus* spp.) (Clayton 1992; Haftorn 1992). Given the existence of anecdotal reports of caching in the wild (Hunt 2000; our pers. obs.), and the facts that almost all corvids cache (Goodwin 1986) and the common ancestors of both the Corvidae family and the *Corvus* genus were almost certainly cachers (unpublished data S. R. de Kort & N. S. Clayton), it is very likely that NC crows do cache food. Caching and tool use are physically similar in that they both involve inserting objects into concavities. Since different motor patterns can develop from the same precursor by differentiation (Berridge 1994), it is possible that caching and TOB might be ontogenetically and/or phylogenetically related – a hypothesis explored elsewhere (unpublished data B. Kenward, C. Schlögl, A. A. S. Weir, C. Rutz, T. Bugnyar & A. Kacelnik).

Ontogeny of Tool Use in Other Species

With the notable exceptions of the woodpecker finch (Tebbich et al. 2001) and the Egyptian vulture (Thouless et al., 1989), previous detailed studies of TOB ontogeny have focussed on primates (e.g. Beck 1978) – although Borsari & Ottoni (2005) also describe an avian TOB thought to result from inherited action patterns. The development of manipulatory behaviour has often been investigated from the perspective of cognitive development, by testing sensitivity to functional aspects of objects (e.g. Hauser et al. 2002; Spaulding & Hauser 2005), or by using conceptual tools such as neo-Piagetian theory (e.g. Poti' & Spinozzi 1994). A similar approach is beyond the scope of this study (we have not yet completed an analysis of Piagetian stages in NC crows).

Longitudinal ethological studies of object manipulation ontogeny in primates show that a long period of object exploration and learning, during which object oriented behaviours become progressively more complex, precedes successful tool use (Fragaszy & Adams-Curtis 1997; Inoue-Nakamura & Matsuzawa 1997; Biro et al. 2003; Lonsdorf 2005; Lonsdorf 2006). It is also known that juveniles from many primate species have a predisposition to perform certain manipulatory action patterns, such as insertion – e.g. chimpanzees, *Pan troglodytes* (Schiller 1952; Hayashi & Matsuzawa 2003); capuchins, *Cebus apella* (Parker & Poti' 1990; Fragaszy & Adams-Curtis 1997); and baboons, *Papio cynocephalus anubis* (Westergaard 1992) – although for many of these studies social influence cannot be ruled out. Fragaszy and Adams-Curtis

(1991), and Parker and Poti (1990), both interpreting their observations of the ontogeny of manipulatory behaviour in capuchin monkeys, concluded that tool use probably develops due to learnt associations between motor patterns (aspects of which are inherited) and their consequences. Fragaszy and Adam-Curtis (1991) point out that the fact that inefficient behaviours are only gradually reduced is more consistent with a behaviourist explanation than with neo-Piagetian processes such as assimilation and accommodation, and the same logic applies to our observation of the continuation of precursor behaviours after directly functional behaviour was established. Our account of NC crow TOB ontogeny in terms of inherited predispositions and the learning of object affordances through exploration that is not externally reinforced therefore corresponds well to accounts of the development of tool use in primates, including humans (Gibson & Pick 2000; Lockman 2000).

Among the most complicated TOBs described in non-human animals is nut-cracking as performed by chimpanzees (Inoue-Nakamura & Matsuzawa 1997; Boesch & Boesch-Achermann 2000; Biro et al. 2003; Hayashi et al. 2005) and capuchins (Fragaszy et al. 2004). Juvenile chimpanzees acquire the skill at about 3.5 years of age, after extensive object exploration since infancy. With respect to manipulation of stones alone, Inoue-Nakamura and Matsuzawa (1997) recorded 21 different fundamental actions – more than twice as many categories of object manipulation as we recorded. This is partly due to unavoidable arbitrariness in categorizing behaviour, but it may also reflect real complexity and be due to the fact that primates are equipped with four five-digit manipulatory appendages, plus a mouth, whereas NC crows make do with a beak and two feet which are less dextrous than chimpanzee hands. Skills like nut-cracking with stones, which involve the positioning of three objects, may be impossible for crows mainly because of differences in anatomy, not cognition (though crows have their own solution to this problem: Hunt et al. 2002). For both twig tool use in NC crows and nut cracking in chimpanzees, although suggestive evidence exists, there is no conclusive proof that the agents have knowledge of the physical forces involved – the behaviours are best accounted for by a combination of inherited predispositions and learnt knowledge of object affordances.

Social Influence

As mentioned already, wild NC crows show some forms of TOB which are more complex than ‘simple’ twig tool use, including manufacture of step-cut pandanus leaf tools (Hunt & Gray 2003) and hooked twig tools (Hunt & Gray 2004a). Furthermore, wild-caught NC crows investigated under controlled conditions in the lab show tool-related skills (Chappell & Kacelnik 2002; Weir et al. 2002; Chappell & Kacelnik 2004) which clearly exceed those observed so far in our hand-raised juveniles. We know that crows can make the simple pandanus tools without the opportunity for observation (Kenward et al. 2005), and it is still possible that given a longer period the juveniles would, by themselves, develop these advanced forms of tool-making. However, the possibility remains that social learning plays a role in the acquisition of more advanced TOB behaviours – specific techniques and tool shapes may be socially transmitted. In the following paragraphs, we critically discuss this possibility.

The results of our object choice experiment show that there is a clear effect of social influence by human foster parents on object manipulation in NC crows – an effect which could be described as either stimulus or local enhancement depending upon whose definitions are used (Galef 1988; Heyes 1994). The preference is robust to the extent that it is displayed not only during demonstrations but also when the demonstrator is no longer interacting with the objects. Preferential attention to objects or sites attended to by tutors could provide a mechanism for wild juvenile NC crows to learn socially which objects are relevant for tool use. It is worth noting, however, that if social transfer is responsible for regional differences in pandanus tool manufacture (Hunt & Gray 2003), it would require a mechanism such as imitation or emulation, which have been demonstrated experimentally in other (non-tool using) bird species (Zentall 2004) but have not yet been explored in this species.

The two tutored birds carried and inserted twigs more frequently than the untutored pair. This effect was found in all sessions, not only in those in which demonstration took place, indicating a lasting after-effect of demonstrations. They also increased twig-related behaviours, as well as insertions of other objects, at a faster rate than the untutored birds. While there are several caveats in the interpretation of these results (two of the subjects were siblings, and the sample was small, meaning that chance genetic or experiential individual differences cannot be ruled out), several lines of evidence suggest that their increased twig carrying and inserting was a result of the tutoring.

Firstly, our social enhancement experiment demonstrated that social influence does affect object choice. Secondly, differences between the tutored and untutored crows appeared in the parameters expected to differ if social learning takes place, but not in other parameters used to measure general development – locomotion and non-food non-twig item carrying. Thirdly, the effects we found were very marked – after two weeks post-branching, both tutored birds carried twigs more than twice as often as either of the untutored birds.

Juvenile NC crows in the wild observe their parents using tools and subsequently use the same tools (Hunt 2000), as do juvenile chimpanzees (e.g. Lonsdorf 2006), but it is unknown how this affects the crows' acquisition of TOB. The only other study investigating the ontogeny of twig-tool use in birds found no effect of social influence (Tebbich et al. 2001). However, social influence on tool use and object choice has been described for a number of primate species (e.g. Fragaszy & Visalberghi 2004; McGrew 2004).

Concluding Remarks

In spite of its uniqueness and complexity, the development of TOB in NC crows has many features in common with the development of other avian behaviours, particularly in evidencing a complex interplay between a rich hereditary endowment, individual learning, and socially-transmitted knowledge. While much remains to be investigated, our observations allow for the elimination of several putative mechanisms of acquisition. In particular, we can exclude the extreme possibilities that TOB is entirely dependent on social inputs (i.e. sustained exclusively by cultural transmission and thus not reflecting a dedicated evolved adaptation), or that it has a purely individual, insight-based origin. Although we do not know yet how important TOB is in the economy of resource acquisition in the wild, it is also unlikely that tools are just a luxury: if they were, we would not see inherited action patterns that must have evolved through selection and are crucial in sustaining TOB in adult crows (see Tebbich et al. 2002 for an investigation of this issue in the woodpecker finch). In terms of cognition, and given NC crows' ability to find creative solutions to novel problems involving tools, it remains a priority to establish if TOB, or the circumstances that led to its evolution, have fostered specially advanced abilities for thoughtful inference.

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TABLES

Table 1. Ethogram definitions of object oriented behaviours in juvenile NC crows

Behaviour category	Behaviour	Description
Touching	Grasping	Contacting an object by placing the beak parts on either side
Touching	Nibbling	Grasping but with open and close or back and forth movements of the beak
Touching	Pecking	Self-explanatory
Touching	Carrying	Grasping an object so it is no longer attached to or supported by a substrate
The following behaviours are all possible only during carrying:		
Precursor action	Rubbing	Rubbing any object against any substrate with at least two (and usually more) back and forth movements (excluding proto-probing, wrong-angle probing, and insertion [below]) (Supplementary video 1)
Precursor action	Proto-probing	Holding a twig in a manner appropriate for probing a hole or crevice, touching it against a substrate which is not a hole or crevice (for example, the side of a perch), and moving it back and forth against the substrate (Supplementary video 2)
Precursor action	Poking	Holding a twig and jabbing the end against any flat substrate
Precursor action	Wrong-angle-probing	Holding a twig and performing motions which could result in an insertion, because the behaviour is directed towards a hole or crevice, but do not because the twig is held at the wrong angle – emerging either sideways or backwards out of the beak
Directly functional action	Inserting	Inserting any object into a hole or crevice. Sometimes this behaviour also includes back and forth head motions which we call ‘probing’, but in practice it is difficult to distinguish between probing and non-probing insertion, so probes were not recorded separately from other insertions

Table 2. Effects of age, treatment group, and individual difference on behaviours in juvenile NC crows.

Response variable	Age		Individual		Treatment group		Age * Individual		Age * Treatment Group	
	$F_{1,264}$	P	$F_{2,264}$	P	$F_{1,264}$	P	$F_{2,264}$	P	$F_{1,264}$	P
Carrying twigs	202.27	**< 0.001**	1.41	NS	115.11	**< 0.001**	3.67	**0.027**	8.88	**0.003**
Inserting twigs	149.01	**< 0.001**	0.22	NS	9.20	**0.003**	14.45	**< 0.001**	99.82	**< 0.001**
Carrying non-food non-twig items	283.19	**< 0.001**	0.14	NS	0.30	NS	17.94	**< 0.001**	0.97	NS
Inserting non-food non-twig items	155.84	**< 0.001**	1.58	NS	0.00	NS	1.19	NS	9.24	**0.003**
Inserting food	124.63	**< 0.001**	1.16	NS	0.41	NS	1.42	NS	10.00	**0.002**
Locomotion	352.13	**< 0.001**	6.19	**0.002**	0.01	NS	11.75	**< 0.001**	1.09	NS

Significant *P* values shown in bold. See methods section for GLM details and Fig. 6 for visualisation.

FIGURES LEGENDS

Figure 1. Photographs of a) a block hole and b) a crevice platform, both with a twig being inserted by Uék. For dimensions see text.

Figure 2. Development of precursor actions (☐) and insertion (■) in four juvenile NC crows. The asterisk indicates the week when successful food retrieval was first observed. Note that, in order to show general development, tutored and untutored birds are pooled (see Fig. 6 for differences between the groups). Error bars indicate standard error. Data points in each week are slightly offset to avoid overlap.

Figure 3. Types of precursor action shown by four juvenile NC crows, showing rubbing (○), proto-probing (■), poking (●), and wrong-angle-probing (☐). Data pooled as in Fig. 2. Error bars indicate standard error. Data points in each week are slightly offset to avoid overlap.

Figure 4. General pattern of development in four juvenile NC crows, showing locomotion (■), object touching excluding carrying (○), and object carrying (☐). Error bars indicate standard error. Data points in each week are slightly offset to avoid overlap.

Figure 5. Object categories touched by four juvenile NC crows. Categories are self-explanatory or defined as follows. Hole: the lip or cavity of any natural or artificial holes and crevices in the aviary. Perch: Any wooden part of the aviary fixtures. Aviary fixture: Any part of the aviary not covered by other categories. Other portable: any non-food non-twig item which the bird could carry (e.g. toys).

Figure 6. Comparison of development in four juvenile tutored and untutored NC crows. Tutored group (solid lines): Uék (●) and Nalik (■); Untutored group (dashed lines): Oiseau (○) and Corbeau (☐). Inset panels show the raw data and model fit for the two groups. Error bars indicate standard error. Panel legends show significant predictors for each dependent variable. For details of statistical model, see text and Table 2.

Figure 7. Juvenile NC crow object preference after witnessing human foster parent manipulating one of a pair of novel objects. The categories are the phases within a trial, in sequence (see method section for details). Bars indicate how often the subject manipulated demonstration target first (■), and most often (☐). Dashed line indicates results expected under the null hypothesis of no effect of demonstration. *N* = 32 (16 trials each for Uék and Nalik, pooled). *P* values are calculated against the chance binomial distribution.

Figure 1

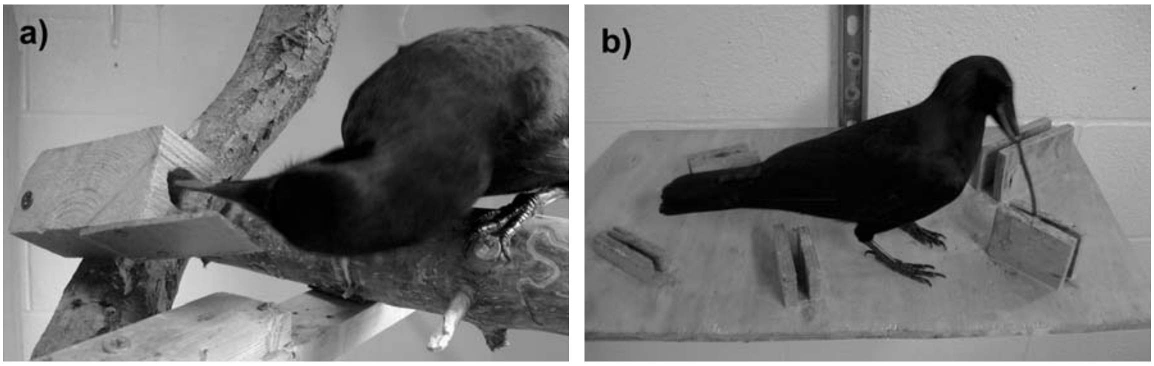


Figure 2

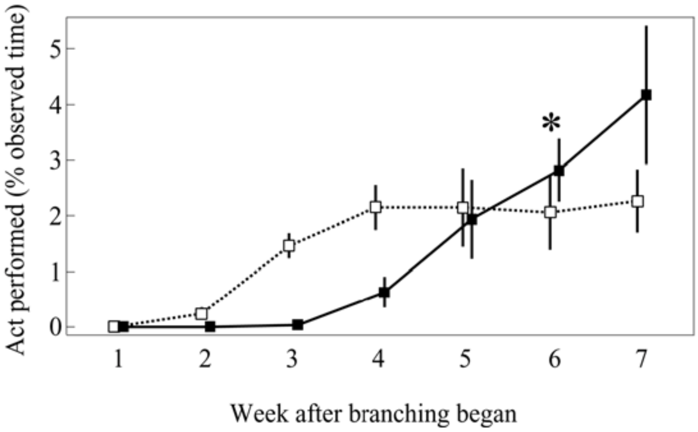


Figure 3

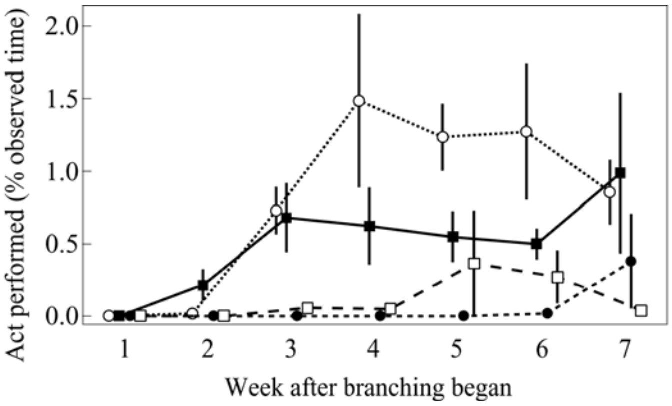


Figure 4

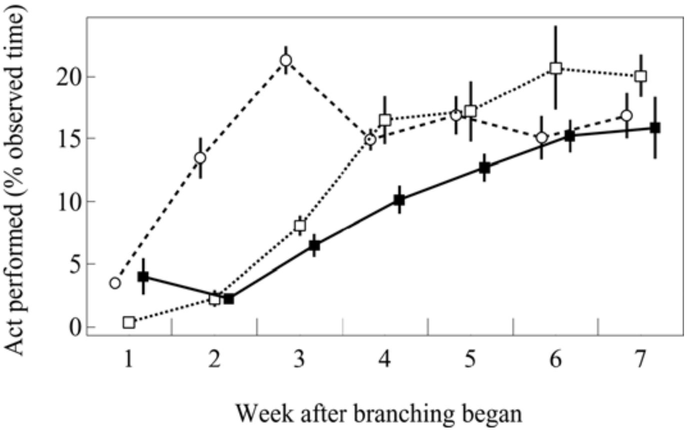


Figure 5

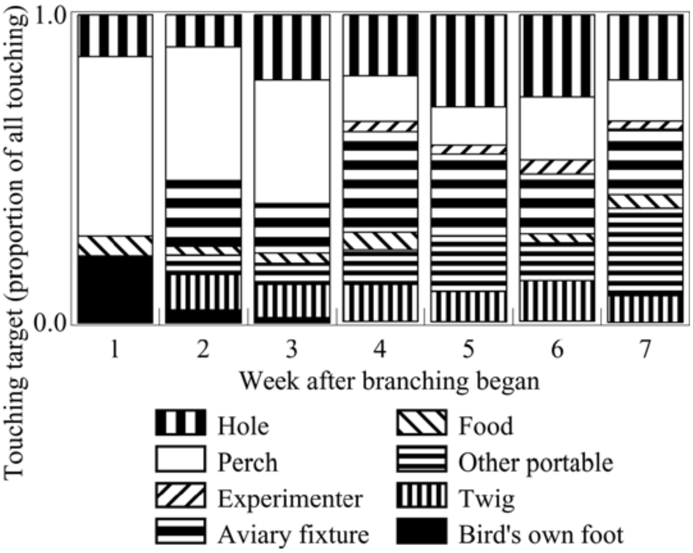
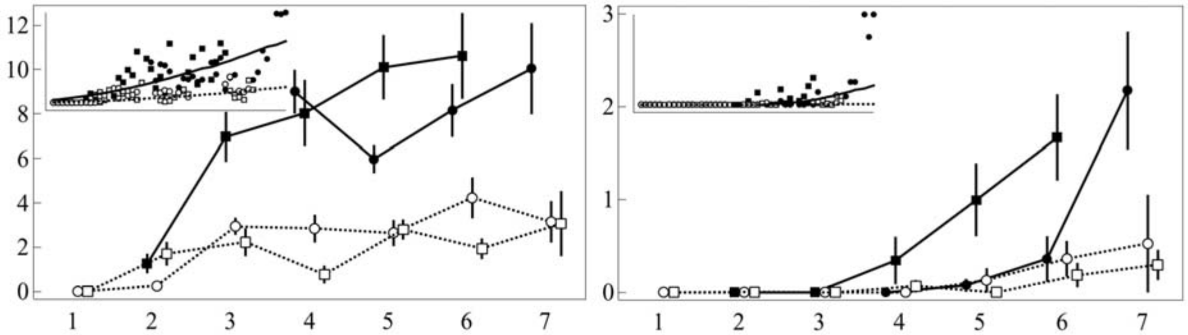
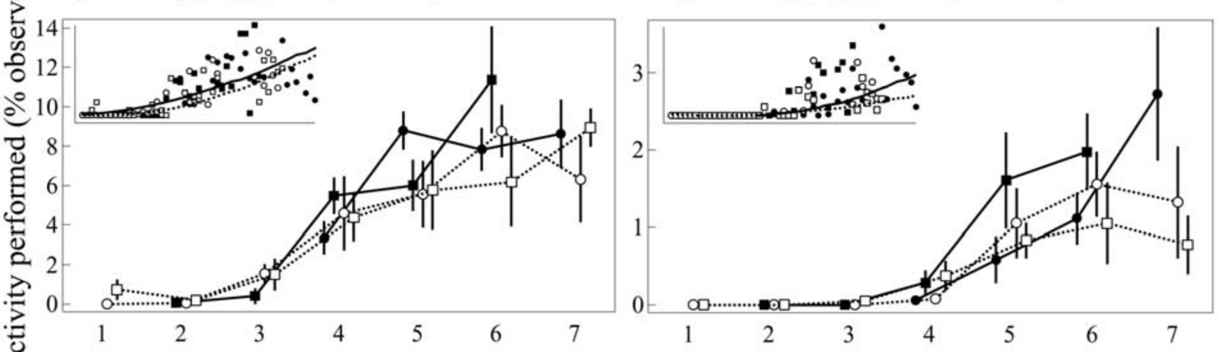


Figure 6



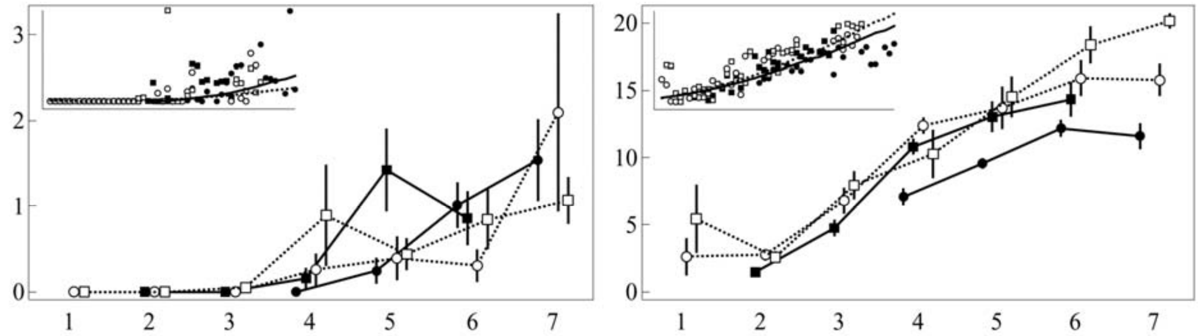
a) Carrying twigs.
Age ($F_{1,264}=202.27$, $P<0.001$),
Group ($F_{1,264}=115.11$, $P<0.001$),
Age * Individual ($F_{2,264}=3.67$, $P=0.027$),
Age * Group ($F_{1,264}=8.88$, $P=0.003$).

b) Inserting twigs.
Age ($F_{1,264}=149.01$, $P<0.001$),
Group ($F_{1,264}=9.20$, $P=0.003$),
Age * Individual ($F_{2,264}=14.45$, $P<0.001$),
Age * Group ($F_{1,264}=99.82$, $P<0.001$).



c) Carrying non-food non-twig items.
Age ($F_{1,264}=283.19$, $P<0.001$),
Age * Individual ($F_{2,264}=17.94$, $P<0.001$).

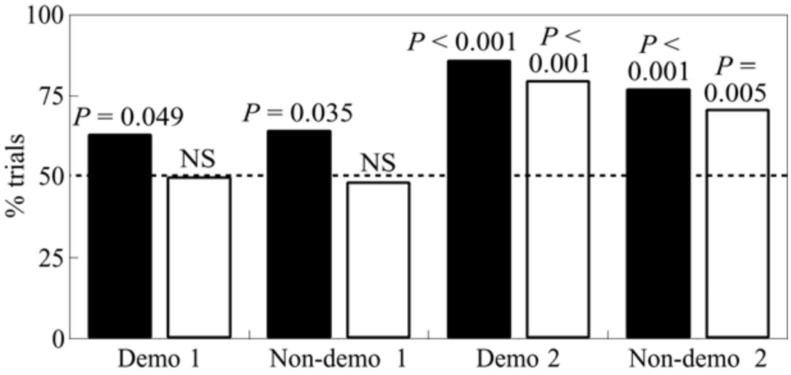
d) Inserting non-food non-twig items.
Age ($F_{1,264}=155.84$, $P<0.001$),
Age * Group ($F_{1,264}=9.24$, $P=0.003$).



e) Inserting food.
Age ($F_{1,264}=124.63$, $P<0.001$),
Age * Group ($F_{1,264}=10$, $P=0.002$).

f) Locomotion.
Age ($F_{1,264}=352.13$, $P<0.001$),
Individual ($F_{2,264}=6.19$, $P=0.002$),
Age * Individual ($F_{2,264}=11.75$, $P<0.001$).

Figure 7


100
75
50
25
0
% trials
P = 0.049
NS
P = 0.035
NS
P < 0.001
P < 0.001
P < 0.001
P = 0.005
Demo 1
Non-demo 1
Demo 2
Non-demo 2