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

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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 aspects of these behaviours are inherited and how they interact with individual and social experience remained unknown. To examine the interaction between inherited traits, individual learning and social transmission, we observed the ontogeny of twig tool use in hand-reared juveniles. Successful food retrieval was preceded by stereotyped object manipulation action patterns that resembled components of the mature behaviour, demonstrating that tool-oriented behaviours in this species are an evolved specialization. However, there was also an effect of social learning: juveniles that had received demonstrations of twig tool use by their human foster parent showed higher levels of handling and insertion of twigs than did their naïve counterparts; a choice experiment showed that they preferred to handle objects that they had seen being manipulated by their human foster parent. Our observations are consistent with the hypothesis that individual learning, cultural transmission and creative problem solving all contribute to the acquisition of the tool-oriented behaviours in the wild, but inherited species-typical action patterns have a greater role than has been recognized.

New Caledonian crows, *Corvus moneduloides*, are renowned for their complex tool-oriented behaviour, which involves both tool use and manufacture. Compared with most other tool-using animals (Beck 1980; Kacelnik et al. 2006), this species stands out with regard to the frequency of tool-oriented behaviour and the diversity and complexity of tool shapes routinely used in the wild (Hunt 1996, 2000; Hunt & Gray 2002, 2004a, b), the ability to select tools appropriate for a given task (Chappell & Kacelnik 2002, 2004) and the capacity to create novel tools according to need (Weir et al. 2002). Furthermore, circumstantial evidence, in the form of regional variation, suggests that 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 tool-oriented behaviour, but until now a detailed study of the process has been lacking. Some of the theoretical questions are similar to and relevant to problems posed by the acquisition of tool-oriented behaviour in all other species, including humans.

The emergence of tool use in the child involves a complex interplay between inherited, individually learned and social factors. The development of this behaviour 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 carried out. 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 that 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 tool-oriented behaviour in humans.

We hand-reared four captive-bred New Caledonian crow chicks under controlled laboratory conditions to investigate the contributions of both social and nonsocial factors in the ontogeny of tool-oriented behaviour in this species. Two crows received regular demonstrations by their human foster parent of how to use twig tools for retrieving

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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 these leaves to make tools. These findings showed that the species has an inherited predisposition for using and manufacturing tools. In this paper, we present detailed ethological data and further analyse the development of tool-oriented behaviour in these individuals, to examine the interaction of inheritance and experience during development and the influence of social inputs. To achieve these goals, we (1) made detailed observations of the development of tool-oriented behaviour to determine more precisely what is inherited, and (2) investigated whether demonstrations of tool use by human foster parents have a measurable effect on the ontogeny of tool-oriented behaviour.

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 more cognitively demanding than the foraging and courtship behaviours that allowed the fish to produce the eggs. However, tool-oriented behaviour may be particularly revealing about processes of physical cognition, because it involves creating relations between two or more external objects in a manner that is easily observable (and amenable to experimental manipulation). Our finding of an inherited predisposition for tool-oriented behaviour in New Caledonian crows (Kenward et al. 2005) raises questions of what is inherited.

Many hypotheses are conceivable, varying in how this 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 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 New Caledonian crow could be equipped with cognitive mechanisms that allow it to learn physical laws by observing object interactions, and then plan goal-directed tool-oriented behaviour that exploits these laws ('insight': Thorpe 1963). The concept of insight itself is problematic, and even ignoring the conceptual difficulties, evidence of insight in nonhuman 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 predict incomplete actions emerging before 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 tool-oriented behaviour emerges because of a general manipulatory tendency coupled with learning, the predictions would depend upon the type of learning. If operant conditioning were 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 that enable them to learn more about the affordances of objects and the environment.

These hypotheses are not mutually exclusive: different processes may be involved at different developmental stages, and different levels of cognition could accompany the performance of externally similar actions. For example, insight is unlikely to precede or cause the early stages of the acquisition of tool use in children (Lockman 2000), but it is obviously available to older individuals. Furthermore, an individual is unlikely to experience insight regarding tool use unless it has tendencies that 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 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 was not to categorize tool-oriented behaviour in New Caledonian crows as the result of one particular process (for instance, deciding whether tool-oriented behaviour is cultural), but to determine as precisely as possible how the complex behaviour of adult New Caledonian crows emerges from the interaction of heritable trends and specific individual and social learning processes (see Bateson 1978, 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 that juvenile woodpecker finches, *Cactospiza pallida*, took to start using tools successfully (Tebbich et al. 2001). Two other tool-oriented behaviours 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 showing that social input was not necessary. For wild New Caledonian crows, however, circumstantial evidence suggests 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, and tool shapes vary regionally in shape and complexity in a manner consistent with cultural transmission (Hunt & Gray 2003). The possibility that aspects of tool-oriented behaviour are culturally sustained would be strengthened if we could show that social influence indeed contributes to the development of tool-oriented behaviour in New Caledonian crows. 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 whether New Caledonian crows matched object choice to that of a human demonstrator.

In summary, although we do not see tool-oriented behaviour as necessarily demanding in cognitive terms, we do 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 have placed the developmental observations of tool-oriented behaviour in the general framework of behavioural development in birds.

METHODS

Subjects and Housing

The subjects were four laboratory-born, hand-reared New Caledonian crows: two male siblings (‘Oiseau’ and ‘Corbeau’), a male named ‘Nalik’ and a female named ‘Uék’. 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 New Caledonian crows in our laboratory. This was the first successful breeding of New Caledonian crows in captivity, and we used all available subjects (wild-bred chicks were unavailable for logistical reasons). Uék was incubated by her parents and removed from the nest at 1 day old. The other subjects came from eggs that had been removed from the nests shortly after being laid and artificially incubated. The chicks were hand-reared 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 an increasing tendency to locomote inside and then outside the nest, so there was no specific fledging point. At 25–26 days old, however, all four birds began to leave the nest and climb around the perches (‘branching’). We took branching, rather than fledging, as the starting point for recording behaviour, because it was at this stage that birds began to locomote and manipulate objects.

Each aviary measured 3.3 × 3.9 m and was 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 pieces of chopped meat and mealworms, most of which were accessible only through tool use.

Additional holes and crevices were used to demonstrate tool use (see below), although 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 on to perches, each in a different position in the aviary (block holes; Fig. 1a). Five crevices (7–11 cm long, 2–6 cm deep, and 4–18 mm wide) were made with pairs of parallel wooden plates and mounted on a wooden platform fixed to the wall (crevice platform; Fig. 1b). Crevice platforms were not installed in the aviaries until midway through the observation period.

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 after fledging, when 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, Purina Pet Care Ltd., New Malden, U.K.; Orlux Universal and Orlux Granules insect and fruit mixes, Orlux nv, Wielsbeke-Ooigem, Belgium; peanuts and mealworms). However, the most preferred food, meat, was available only during hand feeding, by tool

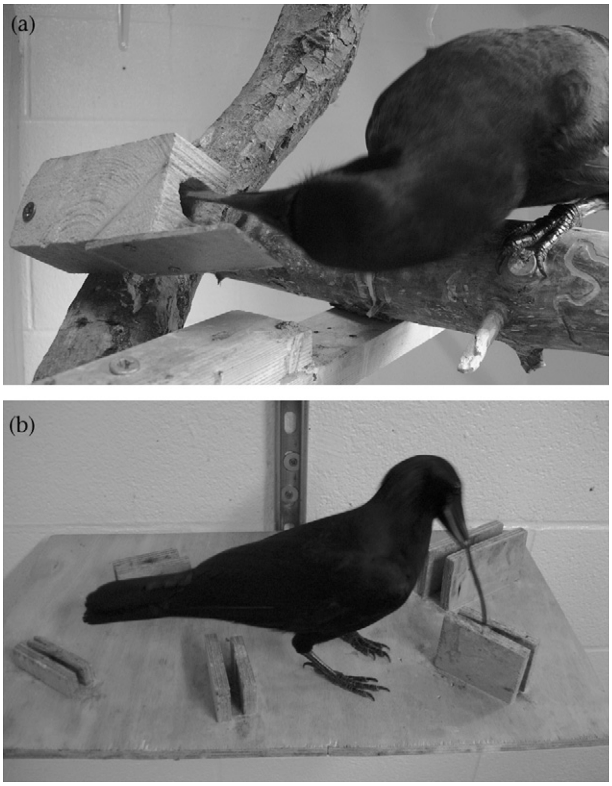

Figure 1. Photographs of (a) a block hole and (b) a crevice platform, both with a twig being inserted by Uék.

use and during experimental and observation sessions. Drinking and bathing water were permanently available. Each bird also had a cage (90 × 60 cm and 80 cm high) inside the home aviary, into which it was placed at night and also sometimes during experimental sessions.

To determine effects of demonstration of tool use by human foster parents while allowing the crows 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 postbranching, 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, this became inevitable owing to the split of the untutored group. However, because the individuals were hand reared, 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 displayed. Based on 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 postbranching (at which time Nalik was 7, Corbeau 1 and Oiseau 0 days postbranching), when regular formal experimental observation sessions began. The ethogram forms an integral and original part of this study, so we report detailed descriptions and definitions of behaviours (see Results).

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 cohoused bird were both placed in their cages, which were then covered so that the birds were unable to observe the experimenter (B.K.) 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, 10 twigs were taken from the floor and five each were 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 min, 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 compared to other behaviour types until the later stages of observation, 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-min 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, so that demonstrations resembled situations for potential social learning observed in the wild, in which juveniles manipulate tools previously used by their parents (Hunt 2000). Supplementary movie clip 1 in Kenward et al. (2005) shows the demonstration procedure. When the birds were 25–49 days postbranching, we made two modifications to this protocol: (1) on two randomly selected demonstrations per session, the food was withheld to encourage the birds to obtain food for themselves, similarly to what has been reported in birds of other species feeding nestlings (Davies 1976); (2) 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 tool-oriented behaviour resulting in food rewards, we therefore presented a food retrieval task that was still naturalistic but that was easier than the block holes because the crevice required a less delicate manipulation of the tool.

Control sessions were as teaching sessions except that, instead of the experimenter retrieving meat from the hole with a tool, no twig was handled, and 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 twiglike objects (such as pens); owing 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 postbranching, but, like Corbeau, Oiseau never witnessed tool use.

New Caledonian 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-h intervals throughout the observation period. Feedings were staggered so that roughly half the sessions took place immediately after feeding, and the other half took place approximately 45 min 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 three 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 postbranching for Uék, 38 for Nalik, 43 for Corbeau and 44 for Oiseau.

Sessions took place between 0730 and 1930 hours, were blocked pseudorandomly so that different types occurred at all times throughout the day, and the different types were spread evenly throughout the period. Before 8 days postbranching, 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. Logistical constraints made it impossible to use a fully balanced design over the entire observation period (most noticeably, no data exist for Nalik in week 7), but the mean numbers of sessions per day were similar for the tutored and untutored groups (tutored group: 0.5 observation sessions/day, 1.2 teaching sessions/day, 0.3 control sessions/day; untutored group: 0.6 observation sessions/day, 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; these experiments have been presented elsewhere (Kenward 2005; 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 normalize errors (Zar 1999). We used general linear models (GLM), using sequential sums of squares (Grafen & Hails 2002). We checked model fit by inspecting diagnostic scatterplots, using standardized residuals (Grafen & Hails 2002). All models were implemented in Minitab 14.1 (Minitab Inc., State College, PA, U.S.A.). 'Treatment group' was included as a factor in some of our GLMs. Because of the limited sample size, results of those analyses cannot be generalized beyond the four subjects investigated.

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, because the behaviours of interest were performed infrequently and proportions were therefore comparatively small (see Results). We also modelled our data with continuous-time Markov chains, which overcome problems of nonindependence inherent in proportional data (Haccou & Meelis 1992); all analyses, however, yielded similar results to the proportional data, and we therefore present proportion results only because of their more intuitive interpretation.

Matching of Object Choice

To examine further the importance of social input, we conducted an experiment into object choice with the two tutored subjects, when they were between 3 and 4 months postbranching (2 months after formal observation and demonstration ended). We used 32 novel objects, mainly small toys and household items that were small enough for a New Caledonian crow to carry. We assigned objects into 16 pairs so that each object in a pair would be of roughly similar attractiveness, based on criteria such as size and shininess.

We assigned a random object from each pair 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 pseudorandomized 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 1 min later the experimenter removed the object's cover and began the session, which consisted of a 1-min demonstration period and a subsequent 3-min period with no demonstration, followed by an additional demonstration and a nondemonstration period (i.e. the sequence was Demo 1, Nondemo 1, Demo 2, Nondemo 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 nondemonstration 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 nontarget object to prevent the subject seeing it manipulated. The sessions were videorecorded 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

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 defined three classes of object manipulation: 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 postbranching, 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

Table 1. Ethogram definitions of object-oriented behaviours in juvenile New Caledonian crows

Behaviour category	Behaviour	Description
Touching	Grasping	Touching 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
Precursor action	Rubbing*	Rubbing any object against any substrate with at least two (usually more) back- and-forth movements (excluding protoprobing, wrong-angle probing, and insertion [below]) (Supplementary Video 1)
Precursor action	Protoprobing*	Holding a twig in a manner appropriate for probing a hole or crevice, touching it against a substrate that is not a hole or crevice (e.g. 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 that could result in an insertion, because the behaviour is directed towards a hole or crevice, but that 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 also includes back- and-forth head motions ('probing'), but it is difficult to distinguish between probing and nonprobing insertion, so probes were not recorded separately from other insertions

*Possible only during carrying.

insertions increased steadily over the remaining observation period (Fig. 2). Of the four precursor behaviours, the most common were 'rubbing' and 'protoprobing' (Table 1, Fig. 3, supplementary videos 1 and 2, respectively). Protoprobing 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.

'Touching' began while locomotion was only beginning to develop, and 'carrying' developed 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 appeared to be protocaching, but we were unable to collect data on whether individuals specifically retrieved food they had hidden.

Comparison of Treatment Groups

We first 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; the four possible interaction terms. Of seven response variables, session type and its interactions were not significant predictors for the following six variables: locomotion, twig carrying, nonfood nontwig item carrying (e.g. toys or wood chips), food

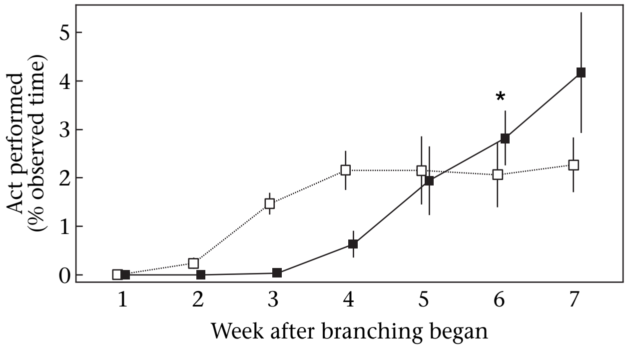

Figure 2. Mean ± SE percentage of time spent in precursor actions (□) and insertion (■) by four juvenile New Caledonian crows as a function of age. Asterisk indicates the week when successful food retrieval was first observed. To show general development, tutored and untutored birds were pooled. Data points in each week are slightly offset to avoid overlap. See Methods for explanation of 'branching'.

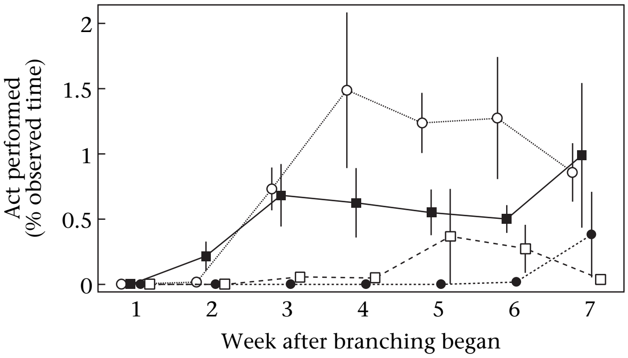

Figure 3. Mean ± SE percentage of time spent in precursor actions shown by four juvenile New Caledonian crows as a function of age, showing rubbing (○), protoprobing (■), poking (●) and wrong-angle probing (□). Data pooled as in Fig. 2. Data points in each week are slightly offset to avoid overlap. See Methods for explanation of 'branching'.

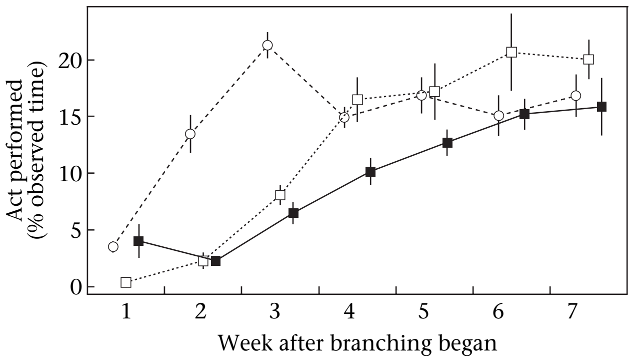

Figure 4. Mean ± SE percentage of time spent in different activities by four juvenile New Caledonian crows, showing locomotion (■), object touching excluding carrying (○) and object carrying (□). Data points in each week are slightly offset to avoid overlap. See Methods for explanation of 'branching'.

inserting, nonfood nontwig item inserting or twig inserting. The only variable that 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 than in observation sessions; this result is somewhat trivial, because 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; the interactions between age and individual, and between age and treatment group (Table 2).

As expected, the frequency of all analysed behaviours increased with age (Fig. 6). More importantly, however, 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 nonfood nontwig 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 nondemonstration periods; in only two of 32 trials did a bird not manipulate both objects at least once (Nalik: $\overline{X} \pm$ SE of 11.4 ± 1.1 bouts of touching per trial, mean duration = 10.1 ± 0.8 s; 5.0 ± 0.9 carrying bouts, mean duration of 8.6 ± 1.5 s; Uék: 11.2 ± 0.7 bouts, duration = 10.7 ± 0.8 s; 8.6 ± 0.9 bouts, duration = 7.7 ± 0.7 s. On six occasions a bird picked up one object and poked the other object with it.

The birds showed a clear preference for the target object (Fig. 7), as measured by both which object they manipulated first and which object they manipulated most often. There was a nonsignificant trend for this effect to increase in the second half of the trial, so that the target object was

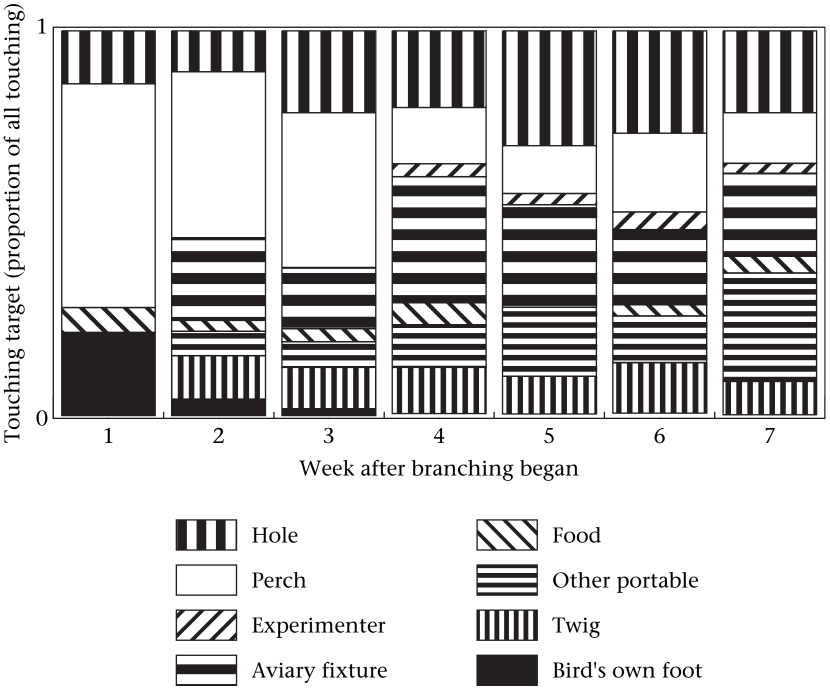

Figure 5. Object categories touched by four juvenile New Caledonian crows. Categories are self-explanatory or defined as follows. Hole: the lip or cavity of any natural or artificial holes and crevices in the aviary. Perch: any wooden part of the aviary fixtures. Aviary fixture: any part of the aviary not covered by other categories. Other portable: any nonfood, nontwig item that the bird could carry (e.g. toys). See Methods for explanation of 'branching'.

not manipulated significantly more often until the demonstration 2 period.

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 nonsnail objects and 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 that 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, 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, but Collias & Collias (1964, 1973, 1984) reported that village weaverbirds, *Textor cucullatus*, begin manipulating nest materials within weeks of fledging and continue to do so until they build their first nest. Kortlandt (1955) described how cormorant chicks, *Phalacrocorax carbo*, still in the nest, perform a quivering movement with the head while holding a twig, a movement that they later combine with a jab that incorporates the twig into the nest. Many nonobject-oriented avian behaviours also develop in a similar manner, such as dustbathing (Larsen et al. 2000) and social display (Groothuis 1993).

In addition to the presence of precursors, the tool-oriented behaviour that we observed in New Caledonian crows has other traits 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 tool-oriented behaviours that we observed in these juveniles are species typical and include stereotyped action patterns, such as protoprobing, which develop in a predictable manner without the need to be 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 contribute to 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 tool-oriented behaviour the description of 'innate'. The term has many problems, 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 that have not been shown to co-occur reliably (Mameli & Bateson 2006). As a result, 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 nonintelligent 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 (Parker & Baars 1990). 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 New Caledonian crows) may be the platform that allows and enhances sophisticated cognitive development (Gibson 1990). In the case of tool-oriented behaviour, we have found that New Caledonian crows do have an inherited developmental program that includes well-defined motor schemes, some of which emerge before their integration in directly functional tool-oriented behaviour. This evidence does not exclude

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

	Age		Individual		Treatment group		Age*Individual		Age*Treatment group	
Response variable	$F_{1,264}$	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 nonfood nontwig items	283.19	<**0.001**	0.14	NS	0.30	NS	17.94	<**0.001**	0.97	NS
Inserting nonfood nontwig 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 for GLM details and Fig. 6 for visualization.

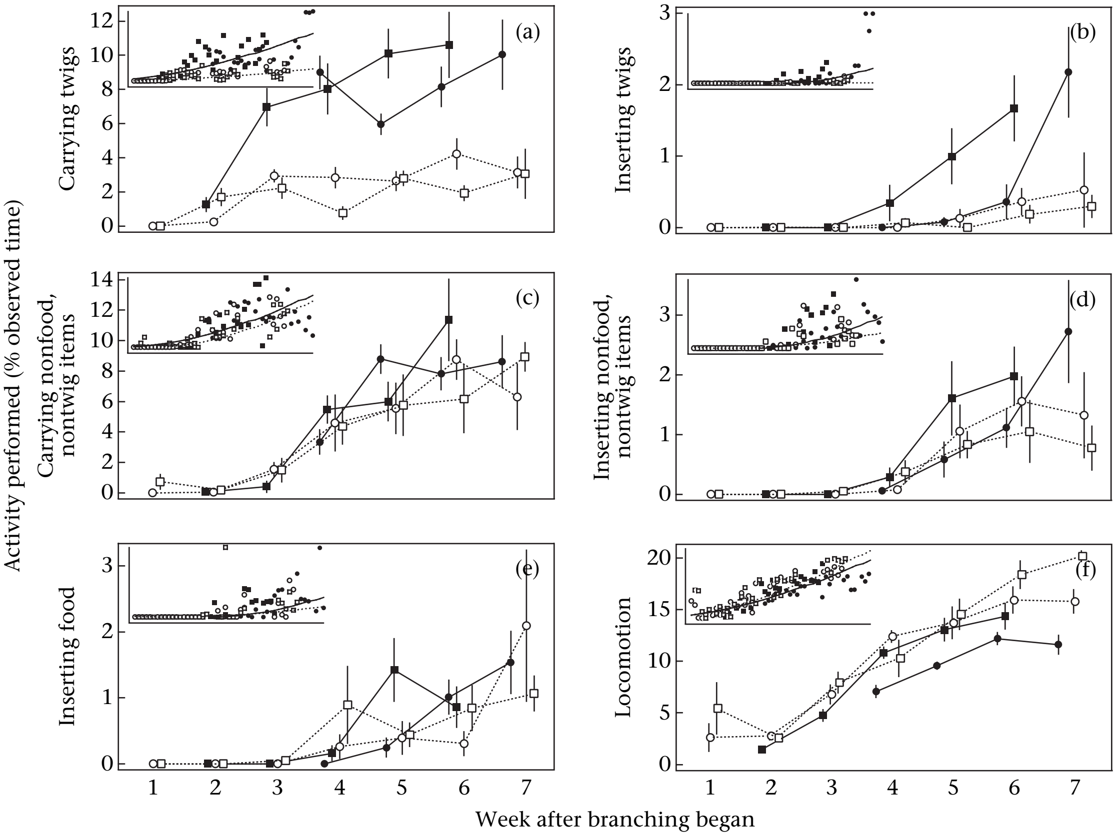

Figure 6. Mean ± SE percentage of time spent in different activities by four juvenile tutored and untutored New Caledonian crows. Solid lines: tutored group, Uék (●) and Nalik (■); dashed lines: untutored group, Oiseau (○) and Corbeau (□). Inset panels show the raw data and model fit for the two groups. Dependent variables and significant predictors are as follows. (a) Carrying twigs: Age, Group, Age*Individual, Age*Group. (b) Inserting twigs: Age, Group, Age*Individual, Age*Group. (c) Carrying nonfood, nontwig items: Age, Age*Individual. (d) Inserting nonfood, nontwig items: Age, Age*Group. (e) Inserting food: Age, Age*Group. (f) Locomotion: Age, Individual, Age*Individual. See Methods for explanation of 'branching'.

the intervention of flexible cognitive processes in the acquisition and/or deployment of the behaviour.

Hansell (2000) has argued that, because nest building rivals New Caledonian crows' tool-oriented behaviour with respect to the diversity of materials used and the complexity of their combination, tool-oriented behaviour 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 from

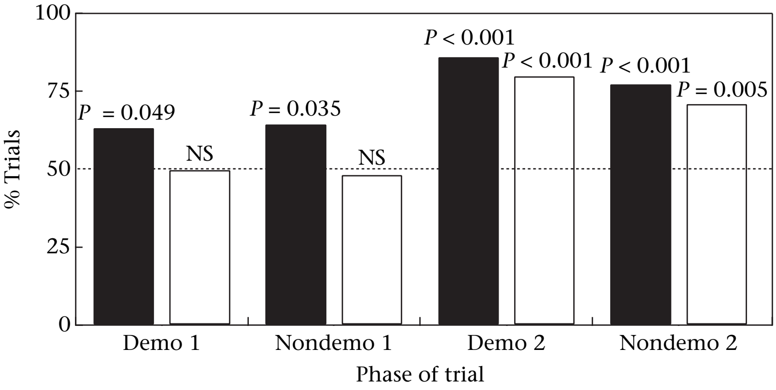

Figure 7. Juvenile New Caledonian crow object preference after witnessing human foster parent manipulating one of a pair of novel objects. The categories are the phases within a trial, in sequence. Bars indicate how often the subject manipulated demonstration target first (■), and most often (□). Dashed 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.

this perspective, nest building may be underestimated in its cognitive sophistication, rather than tool-oriented behaviour being overrated.

The inherited component that we observed in the development of tool-oriented behaviour opens the possibility that regional differences in tool manufacturing, especially those shown for tools made with pandanus leaves (Hunt & Gray 2003), could be the result of genetic differences. This possibility requires some attention before conclusions about cultural transmission are accepted, especially given 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 tool-oriented behaviour. However, behaviour performed by juveniles that 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). Among 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: 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 that it was exposed to pandanus leaves (Kenward et al. 2005). Experimental manipulation can even cause precursor behaviours to be replaced earlier by the directly functional behaviour. Testosterone administration can cause gull chicks, which perform precursor versions of aggressive social displays, to perform the full display (Groothuis 1989; Baerends 1990). The 'precursor' label is thus just descriptive, and the function of such behavioural patterns should be investigated, before assuming that they serve to prepare the adult's version of the behaviour.

The precursor behaviours, however, are likely to serve some function. Hogan (1994, 2001) 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). Tool-oriented behaviour in New Caledonian crows can fit this idea. The motor mechanisms that will later result in hole probing are initially performed in the absence of the stimulus provided by holes, resulting in protoprobing. 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 spadiceus*, 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 precursor behaviours in New Caledonian crows might be to learn about the consequences of object manipulation. Clearly, they cannot learn how to extract food from protoprobing. However, just as 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 an object into another solid object is possible only 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 early in development, has also been described as perception–action development, and has been argued to be fundamental to 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, such as 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 New Caledonian crows requires additional experiments, but the idea provides a good framework to think about, for example, the emergence of insertion out of protoprobing. 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 their attempts 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 emphasized by traditional accounts of perception–action learning; however, the crows persisted in performing actions without food reward long after they had probably learned their consequences, which means that object insertion is also likely to be rewarding. A similar process could also explain the occurrence of precursor action patterns; perhaps what are inherited are not developmental programs for motor patterns, but rather tendencies to find certain actions rewarding.

Perception–action learning may also be important in the acquisition of more sophisticated forms of goal-directed control, such as learning the relation 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, 2004; Weir et al. 2002). 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, page 82) defined play as 'repeated, incompletely functional behavior 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; our wild-caught adults also frequently show apparently functionless behaviour, such as inserting stones into holes in logs and repeatedly breaking pieces of wood. 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), so the play observed in New Caledonian crows could enable them to learn the wide range of tool-oriented behaviours displayed by the species in natural circumstances. Our subjects sometimes engaged in playful behaviours that 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 while running on the ground pushing the tube along in front. These observations support the hypothesis that behaviour that allows the learning of object affordances is inherently rewarding.

Caching

Our observations that food was frequently inserted and left in holes supports the hypothesis that New Caledonian crows are a caching species, although we did not record whether the birds retrieved food after a long enough period for this result to be conclusive. Inserting and quickly retrieving food is a precursor to caching in titmice, Paridae (Clayton 1992; Haftorn 1992). Given the existence of anecdotal reports of caching in the wild (Hunt 2000; B. Kenward, C. Rutz, A. Weir & A. Kacelnik, personal observations), and that almost all corvids cache (Goodwin 1986) and that the common ancestors of both the Corvidae family and the *Corvus* genus were almost certainly cachers (de Kort & Clayton 2006), it is likely that New Caledonian crows do cache food. Caching and tool use are physically similar in that they both involve inserting objects into concavities. Different motor patterns can develop from the same precursor by differentiation (Berridge 1994), so it is possible that caching and tool-oriented behaviour might be ontogenetically and/or phylogenetically related (B. Kenward, C. Schlögl, A. A. S. Weir, C. Rutz, T. Bugnyar & A. Kacelnik, unpublished data).

Ontogeny of Tool Use in Other Species

With the exceptions of the woodpecker finch (Tebbich et al. 2001) and the Egyptian vulture (Thouless et al. 1989), previous detailed studies of the ontogeny of tool-oriented behaviour have focused on primates (e.g. Beck 1978), although Borsari & Ottoni (2005) also described an avian tool-oriented behaviour, in hyacinth macaws, *Anodorhynchus hyacinthinus*, 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. Potì & Spinozzi 1994). However, a similar approach was beyond the scope of this study.

Longitudinal ethological studies of object manipulation ontogeny in primates show that successful tool use is preceded by a long period of object exploration and learning, during which object-oriented behaviours become progressively more complex (Fragaszy & Adams-Curtis 1997; Inoue-Nakamura & Matsuzawa 1997; Biro et al. 2003; Lonsdorf 2005, 2006). Furthermore, juveniles from many primate species have a predisposition to perform certain manipulatory action patterns, such as insertion (chimpanzees, *Pan troglodytes*: Schiller 1952; Hayashi & Matsuzawa 2003; capuchins, *Cebus apella*: Parker & Potì 1990; Fragaszy & Adams-Curtis 1997; baboons, *Papio cynocephalus anubis*: Westergaard 1992), although for many of these studies social influence cannot be ruled out. Fragaszy & Adams-Curtis (1991) and Parker & Potì (1990), both interpreting their observations of the ontogeny of manipulatory behaviour in capuchin monkeys, concluded that tool use probably develops from learned associations between motor patterns (aspects of which are inherited) and their consequences. Fragaszy & Adams-Curtis (1991) pointed out that evidence that inefficient behaviours are only gradually reduced is more consistent with a behaviourist explanation than with neo-Piagetian processes such as assimilation and accommodation. The same logic applies to our observation that the crows continued precursor behaviours after directly functional behaviour was established. Our account of the ontogeny of tool-oriented behaviour in New Caledonian crows, 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 tool-oriented behaviours described in nonhuman 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 & Matsuzawa (1997) recorded 21 fundamental actions, more than twice as many categories of object manipulation as we recorded. This difference is partly due to unavoidable arbitrariness in categorizing behaviour, but it may also reflect real complexity and be because primates are equipped with four five-digit manipulatory appendages and a mouth, whereas New Caledonian crows make do with a beak and two feet that are less dextrous than chimpanzee hands. Skills such as nut cracking with stones, which involve the positioning of three objects, may be impossible for crows, mainly because of differences in anatomy, not cognition (although crows have their own solution to this problem: Hunt et al. 2002). For both twig tool use in New Caledonian crows and nut cracking in chimpanzees, although suggestive evidence exists, there is no proof that the agents have knowledge of the physical forces involved. The behaviours are best accounted for by a combination of inherited predispositions and learned knowledge of object affordances.

Social Influence

As mentioned already, wild New Caledonian crows show some forms of tool-oriented behaviour that 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 New Caledonian crows investigated under controlled conditions in the laboratory show tool-related skills (Chappell & Kacelnik 2002, 2004; Weir et al. 2002;) that exceed those observed so far in our hand-reared juveniles. Crows can make the simple pandanus tools without the opportunity for observation (Kenward et al. 2005), and given a longer period, the juveniles may, by themselves, develop these advanced forms of tool making. However, the possibility remains that social learning contributes to the acquisition of more advanced tool-oriented behaviours; specific techniques and tool shapes may be socially transmitted. In the following paragraphs, we discuss this possibility.

The results of our object choice experiment show an effect of social influence by human foster parents on object manipulation in New Caledonian crows, which could be described as either stimulus enhancement or local enhancement, depending upon whose definitions are used (Galef 1988; Heyes 1994). The preference was robust to the extent that crows displayed it not only during demonstrations, but also when the demonstrator no longer interacted with the objects. Preferential attention to objects or sites attended to by tutors could provide a mechanism for wild juvenile New Caledonian crows to learn socially which objects are relevant for tool use. However, 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, both of which have been demonstrated experimentally in other, nontool using bird species (Zentall 2004) but which have not yet been explored in this species.

In the present study, the two tutored birds carried and inserted twigs more frequently than did 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. The tutored birds also increased twig-related behaviours, as well as insertions of other objects, at a faster rate than did the untutored birds. There are several caveats to the interpretation of these results: two of the subjects were siblings, and the sample was small, so we cannot rule out chance genetic or experiential individual differences. However, several lines of evidence suggest that the increased twig carrying and inserting was a result of tutoring: (1) our social enhancement experiment showed that social influence does affect object choice; (2) 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, i.e. locomotion and nonfood, nontwig item carrying; (3) the effects we found were marked: after 2 weeks postbranching, both tutored birds carried twigs more than twice as often as either of the untutored birds.

The mechanism responsible for the difference between the groups is a topic for further research; the careful controls necessary to reveal mechanistic details of social learning were not practical in this exploratory study. Potential mechanisms range from those involving exposure to conspecifics' changes to the environment (e.g. the socially transmitted skill of pine cone stripping in black rats, *Rattus rattus*, can be acquired from exposure only to half-stripped cones: Zohar & Terkel 1991) to those involving imitation of motor patterns. An explanation based solely on exposure to changes in the environment cannot be ruled out by this study, because only the tutored group was exposed to meat in close association with twigs, but this account seems unlikely given the results of the social enhancement experiment.

Juvenile New Caledonian 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 observation affects the crows' acquisition of tool-oriented behaviour. The only other study of the ontogeny of twig tool use in birds showed 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 tool-oriented behaviour in New Caledonian crows has many features in common with the development of other avian behaviours, particularly in showing a complex interplay between a rich hereditary endowment, individual learning and socially transmitted knowledge. Although 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 tool-oriented behaviour depends entirely on social inputs (i.e. is sustained exclusively by cultural transmission and thus does not reflect a dedicated evolved adaptation), or that it has a purely individual, insight-based origin. Although we do not yet know the importance of tool-oriented behaviour 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 that are crucial in sustaining tool-oriented behaviour in adult crows (see Tebbich et al. 2002 for an investigation of this issue in the woodpecker finch). In terms of cognition, and given the ability of New Caledonian crows to find creative solutions to novel problems involving tools, a research priority is to establish whether tool-oriented behaviour, or the circumstances that led to its evolution, have fostered specially advanced abilities for thoughtful inference.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.anbehav.2006.04.007.

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