

THE ONTOGENESIS OF INNOVATIVE TOOL USE IN AN AMERICAN CROW
(*Corvus brachyrhynchos*)

By

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"In our next lives, we'll remember not to be human.

We'll be a pair of wild geese,

flying high in the sky.

And from that distance,

we'll look down on the world's blinding snows,

it's oceans, waters, hills,

clouds, and red dust,

as if we had never fallen."

N'Guyen-Khac-Hieu

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Abstract

The genus *Corvus* (crows, ravens, rooks and jackdaws) is distinguished among avian tool users by the sheer quantity and diversity of their tool use acts. However, almost nothing is known about how these behaviors develop. This six-year study traced tool use ontogenesis in a single American Crow (*C. brachyrhynchos*) to determine if and to what extent innate behaviors, social, asocial, or insightful learning processes contributed to the development of specific tool use acts. Over the course of the study, Loki spontaneously developed five kinds of tool use involving five different objects. He used a small Frisbee, a water-bottle nozzle, and a plastic cup to acquire and transport water, food, and other objects; he moved a lightweight tripod perch in a way that allowed him to access a previously out of reach item; and he secured a plastic Slinky to his perch and used the free end as a headscratcher. It was found that social learning, in the form of movement imitation, was not a contributing factor in the development of any of Loki's tool use acts. Additionally, the lengthy incubation periods (5 -16 months) and incremental behavioural changes that hallmarked the development of Loki's tool use, were inconsistent with insightful, or cognitive, explanations. It is concluded that these complex, innovative, tool use behaviors developed via the modification of species-typical crow behaviors, such as caching, food soaking, and object-directed play, through instrumental learning mechanisms (Thorndikian conditioning, operant conditioning, and skill learning). Finally, contrary to most reports of avian tool use, much of Loki's tool use was not subsistence-oriented. Furthermore, his object-directed play has persevered with familiar items over several years. Thus, it is proposed that, in some instances, object-directed play may qualify as a form of tool use for which the effects are simply less tangible to the casual observer than acts of subsistence-related tool use.

List of Abbreviations and Symbols Used

BA	Bath
BO	Bowl
CB	Cross Beak
CD	Cap Down
CU	Cap Up
DP	Dry Pan
DE	In or Near Den
FR	Frisbee
GC	Green Plastic Cup
GR	Green Plastic Ring
MF	Mid-Floor
NB	Near Bath
ND	Near Door
NP	Near Perch
PA	Near Dry Pan
sd	Sample Standard Deviation
UC	Under Chair
X	Sample Mean

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Chapter 1

Animal Tool Use and its Ontogenesis

Tool use has been reported in at least one species in every extant vertebrate group except reptiles and amphibians, and in four invertebrate groups (Beck, 1980). How one defines tool use can have a considerable effect on which acts qualify and therefore which animals are considered tool users. Several definitions, or partial definitions, can be found in the literature addressing tool use in non-humans. In his classic book *Animal Tool Behavior*, Beck provides the following:

“... tool use is the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool” (Beck, 1980).

By Beck’s own admission the definition is not perfect. Nonetheless, twenty-four years after its formation, it is still the best option for capturing the essence of what must occur, and how it must occur, for an act to be recognized, and agreed upon by independent observers, as tool use.

Tool use versus proto-tool use

Beck’s definition excludes many behaviors that look like tool use but don’t quite manage to fulfill the stringent definition. In some cases, the object is attached and therefore cannot be held or carried by the user. For example, dropping shellfish from a height onto a rocky substrate, thus breaking open their tough shells, is a notable food-exploitation maneuver. But the act does not qualify as tool use because the user does not wield the rocky substrate. It is,

nonetheless, an intriguing behavior that might be an evolutionary or behavioral precursor for other types of tool use and has been called *borderline* or *proto-tool use*.

Kinds of Tool Use

Tool use can be categorized with varying degrees of specificity by focusing upon different aspects of the act. Categories can reference the broader behavior in which the animal was engaged when it was observed using the tool, such as feeding or grooming ¹, the action that was performed while using the tool, such as prying or wiping ^{2,3}, the actual tool object, such as stick or stone, the tool use outcome, such as eggshell breakage or grub extraction, or by the behavioral origin of the act, be it innate, learned or some combination of the two.

The Origins of Specific Acts of Tool Use

Aside from primate studies, relatively little research has focused on how tool use develops. It might be tempting to presume that tool use is associated with high brain to body weight ratios (surplus encephalization), or complex, centrally coalesced nervous systems. However, animals with relatively simple nervous systems, such as insects and crustaceans, also engage in tool use. For

¹ “feeding, drinking, play, body care, display, aggression, sociality” (Boswall, 1977)

² “unaided throwing; dragging, slapping, rolling, or kicking; aimed throwing; dropping or throwing down; brandishing or waving; clubbing or beating; prodding or jabbing; reaching; pounding or hammering; inserting and probing; prying or applying leverage; digging; balancing and climbing; propping and climbing; stacking; hanging and swinging; absorbing or sponging; wiping; draping or affixing; containing; and baiting” (Beck, 1980, p.13-14)

³ “goad; poker; lever (or crowbar); spear (or lance); rake; cudgel; hammer; baler; brush; scratcher; towel; sponge; sponge, wedge and stopper; thrown missile; dropped missile; anti-skid device; object used to attract attention” (Boswall, 1977)

example, female digger wasps (*Ammophila* sp.) pound the soil sealing their egg-burrows with pebbles or other objects, presumably to reinforce their security.

Ant-lions (the larvae of the genus *Myrmeleon*, a neuropteran fly) and worm-lions (larvae of the genera *Vermileo* and *Lampromyia*, dipteran flies) throw sand with their head and mandibles at prey attempting to escape their pitfalls. Ants of two genera (*Aphaenogaster rudis*, *A. treatae*, *A. tennesseensis*, *A. fulva* and *Pogonomyrmex badius*) place bits of vegetation, wood, mud and sand on top of soft, sticky foods, which they later retrieve and carry back to the colony, which can result in a 10-fold weight increase in the quantity of food acquired (Fellers & Fellers, 1976). Remarkably, invertebrate tools are not restricted to inanimate objects. *Melia tessellata*, a marine crab, detaches small sea anemones and outfits itself by holding one in each cheliped. *Melia* consumes food ensnared by the anemones, as well as extending and waving its chelipeds during locomotion, or if disturbed. The anemones appear, in the latter case, to defend and protect by discharging stinging nematocysts (Duerden, 1905).

The question naturally arises as to *how* such elaborate behaviors come to exist in an animal population. This question is often entertained at the group level, but might be addressed more manageably first at the individual level. For this purpose, an idealized, theoretical, continuum-of-acquisition can be imagined. At one extreme are acts of tool use that are purely innate in origin (genetically transmitted) and at the other end are acts of, for want of a better term, pure cognitive creation. In between are acts that have been acquired through various kinds of learning.

Genetic Transmission

Water-shooting is a prey-capture maneuver in which archer fish (*Toxotes* and *Colisa sp.*) shoot streams of water, up to three meters long, at invertebrate prey located above the waterline. Observational experience is not required for development, and shooting does not appear to have any learned components or to benefit from practice (Timmermans & Vossen, 2000). Water-shooting appears then to be a purely innate tool use act. Innate origins have also been found in the tool use of some higher vertebrates. Owings and Coss found that the sand-kicking California ground squirrels (*Ostomys sp.*) direct towards snakes during mobbing also develops with no prior experience. They conclude that the behavior “is mediated by a strong genetic component” (Owings & Coss, 1977).

When a tool use behavior is present at the species or sub-species level, is executed in a fairly stereotypical manner and occurs even in isolation-reared individuals, then a species-specific, genetic determinant must be making a large contribution. In some cases it may be the only necessary factor aside from the eliciting stimulus.

Social Transmission

Other tool use behaviors develop only after the animal has seen the behavior performed by others. Some of the most compelling examples involve different chimpanzee groups or communities that engage in different types or forms of tool use that remain persistent across generations (termite-fishing with twigs versus termite mound-smashing with sticks). Many acts of tool use by enculturated or captive chimpanzees, orangutans and gorillas have never been

documented in their wild counterparts (McGrew, 1992; Russon & Galdikas, 1993). In cases such as these, one or more of the numerous processes of increasing complexity that operate under the umbrella of social transmission must be at work.

Imitation is the social learning process that probably comes to mind quickest when thinking of ways in which a new behavior might come to exist in an individual's behavioral repertoire. Which animals can and cannot imitate movement is currently a controversial topic among researchers. It is generally agreed though that imitation is a complex, and relatively rare, form of learning, and its prevalence among animals other than great apes is in debate. Imitation will be addressed again in Chapter 2. However for now, it can simply be stated that imitative tool use would manifest as the appearance of the gross behavioral components of the act being produced only after having seen another perform them, and should only occur in animals that are also known to be capable of movement imitation not involving objects. It seems unlikely that one could imitate a movement that incorporates an object if one is unable to imitate movement alone. Moore identified several simpler, non-imitative, processes that should be ruled out when searching for the origins of apparently imitative behavior⁴ (1992; 1996). These same simpler processes should also be considered when searching for the origins of ostensibly imitative tool use.

⁴ Moore (1992) identified the following simpler processes that can appear imitative: normal maturation, local or stimulus enhancement, audience effects, behavioral contagion, environmental after-effects of another's performance, Pavlovian conditioning, observational conditioning, instrumental learning, circular reactions, and finally non-vocal mimicry which was later renamed percussive mimicry (Moore, 1996).

For example, *behavioural contagion*⁵ and *audience effects*⁶ are two relatively simple processes that can induce behavior in an observer that appears similar to that of the performer. Examples of behavioral contagion include an increase in consummatory behavior in satiated chicks, reduction of restlessness in hungry chicks when placed with satiated chicks (Katz, 1937), the sudden seemingly instantaneous flight of flocks of birds and yawning in humans. The spread of milk bottle opening by chickadees, while not tool use, is nonetheless a remarkable phenomenon finally attributed in large part to audience effects (Moore, 1992; Sherry & Galef, 1984, 1990). In these cases an observer has not learned anything about how to behave; instead pre-existing behavior has been elicited merely by the presence of others.

Stimulus enhancement (Spence, 1937) and *local enhancement* (Thorpe, 1956) refer to situations in which an observer has been drawn to an object or a location as a result of the presence of others. In these cases, the performer's behavior has served merely as an attractor, not an example. The observer has learned where to go or what to manipulate, but not how to behave once there or how to manipulate the object to which it was attracted.

Slightly more complex forms of social transmission do actually involve the observer learning something about specific objects or the environment. For

⁵ *Behavioral contagion* has also been called *instinctive imitation*. Its unique characteristic is that the eliciting stimulus is the same as that which it elicits (Moore, 1992; Thorndike, 1898; Morgan, 1896).

⁶ The term *audience effects* is from Moore (1992), and describes situations in which "the mere presence of other animals may potentiate certain reactions". Examples include the increase in chickadees' likelihood of opening containers while in the presence of other chickadees, regardless of whether they have observed the others actually opening containers or not (Sherry & Galef, 1990).

example, *observational conditioning* is defined as a form of associative learning in which a model's behavior labels a relevant object as food or predator, and an observer subsequently directs species-typical behaviors towards it after having been exposed to the performer's reaction. What to eat or avoid eating, what to fear (Cook & Mineka, 1990), and where to direct mobbing behavior can be learned in this way, as is the case with European blackbirds (Curio, Ernst, & Vieth, 1978), and is quite likely so as well in the case of the mobbing behavior of the California ground squirrels described above. Once again, however, how to eat, react fearfully, or mob is not learned; only where or towards what to direct these pre-existing behaviors. Thus in the case of the squirrels, how to kick sand has not been learned, only where to direct it.

None of the processes described above allow for learning how to behave, though they could still be contributors in the acquisition of new behavior. Thus it remains to be seen if they can be identified as causal components in any cases of socially transmitted tool use.

Cognitive Processes

Complex cognitive processes have been suggested, especially in the primate literature, as possible effectors of tool use. One such process is *emulation* (Tomasello, 1996; Tomasello, Davis-Dasilva, Camak, & Bard, 1987) or emulation learning. It is essentially the cognitivist's version of what could happen during situations that appear to be, to the behaviorist, local or stimulus enhancement. Rather than learning where to go, or what to manipulate, the observer learns something about the environment or the object as a result of

having seen others engaging in location- or object-related behavior. It must be stressed that, in this view, the observer does not attend to the behavior of the performer, nor to the result of the performer's actions, but instead learns about the characteristics or *affordances* of the place or thing in such a way that the observer is now better prepared to produce a similar result, by knowing that such a change is possible (i.e., tough nuts can be cracked). “... *in emulation learning, the learner observes and understands a change of state in the world produced by the manipulations of another ...*” (Tomasello, 1996). Subclasses of emulation have also emerged, such as *goal emulation* (Whiten & Ham, 1992) where the learner understands the goal of another's act and reproduces that, in a same or different manner from the original performer.

While many pages of description could be devoted to the varied flavors of cognitive explanations that have been proposed for socially transmitted primate tool behavior, in the interest of brevity here and parsimony overall, appealing to them is best left until all simpler explanations have been exhausted.

Innovative Tool Use

Beyond innate and socially acquired tool use are acts of pure innovation. Innovation, as it is used here, does not refer to a form of learning or a cognitive characteristic, but simply to acts that are resourceful and unique. Therefore, for an act of tool use to be considered an innovation, it must be an original, individual development not acquired through genetic or socially transmitted mechanisms. Innovations may instead come about through trial and error or insightful learning.

Trial and Error Learning

The term “trial and error” is often used to distinguish behavior that cannot be traced to innate or social learning processes. It has come to function as a catch-all phrase that relieves the user from having to clarify which of the many learning processes might be involved in the behavior in question. These include Thorndikian conditioning⁷, operant conditioning⁸, and skill learning⁹, all of which can be responsible for the modification of behavior.

Insightful Learning

Innovation can also come about through what has been called *insightful learning*. Insight was first proposed as a possible factor in the development of animal tool use by Wolfgang Köhler (1927). In the most well known of his studies, Köhler created situations in which chimpanzees were faced with barriers to their food. In some instances bananas were left out of reach outside the animal’s enclosure, or hung on the ceiling high enough so as to be unreachable. Sticks and boxes were also present. Chimps were reported to have solved the height problem by stacking boxes and using them as a ladder, or even climbing upon a keeper’s body. In the most publicized instance, a chimpanzee named

⁷ *Thorndikian conditioning* comes about through the reinforcement of species-typical, reinforcement-appropriate responses, which have been elicited by environmental stimuli (Moore, 2004).

⁸ *Operant conditioning* is defined as the reinforcement of novel (species-atypical) responses (Moore, 2004).

⁹ *Skill learning* is characterized as “a higher form of operant conditioning that requires implicit, rather than explicit, reinforcement” in which “novel responses are learned without external reward” (Moore, 2004).

Sultan, after several failed attempts to reach bananas that were located outside his cage by poking each of the two bamboo sticks through the cage bars, fitted the two sticks together to make one long stick and easily retrieved the food.

In contrast to trial and error learning, Köhler described what he saw as insightful learning and proposed that this was a unique learning process, which involved the performer's *comprehension* of critical relationships followed by the sudden, physical, solution to a problem. Given that comprehension cannot yet be observed directly, the best evidence that problem-related insight has occurred must come in the form of a naïve individual exhibiting a lack of overtly related behavior prior to the execution of a sudden and successful solution to a sufficiently novel problem.

Köhler's postulation of animal tool use arising from a purely cognitive source predated the cognitive revolution in studies of animal behavior by some 60 years. Unfortunately, Köhler's studies were found lacking in the controls necessary to rule out prior physical and/or observational experience as a confounding factor. It has been suggested that Kohler's chimps witnessed others (possibly even humans) engaging in similar acts (Schiller, 1957), and that Sultan's performance was first produced in play and used shortly thereafter (Chance, 1960). This makes it impossible to determine whether Sultan's act was one of imitation or trial and error learning rather than insightful innovation.

The origins of Sultan's tool use may have been even simpler still. Schiller proposed that "unlearned motor patterns" play a role in the development of chimpanzee tool use. In a comparable study, he found that 19 out of 20 adult

chimps, given sticks with hollow ends and acting in the absence of bananas to retrieve, fitted the sticks together within five minutes of having received them, and that their initial object-directed behaviors (drawing in, licking, smelling, chewing) were the same as those in which Sultan engaged. He observed that several exploratory behaviors including licking, chewing, poking, hammering and "... thrusting the end into any available openings" occurred frequently and "constitute the basis of complex motor patterns of utilizing sticks as tools" (Schiller, 1957).

The observation that chimps playfully join and attempt to poke sticks into holes - a behavior that is not much different from poking twigs into termite mounds - suggests that this behavior may be but one of several inherited determinants that combined to produce Sultan's joining of the sticks, and other chimpanzee tool use acts as well.

The question of whether non-human primates possess the ability for causal understanding continues to be explored. Sadly, even in these most promising animal subjects, and after almost 100 years of research, positive evidence is scant (Povinelli, 2003; Povinelli & Vonk, 2003, 2004; Tomasello & Call, 1997; Visalberghi & Tomasello, 1998). Nonetheless, primate tool use garners an overwhelming amount of research interest, no doubt because it has the potential to portend something about the evolution of human tool use. However, as a group, birds easily contend with apes in the sheer quantity and diversity of their tool use, and they do so with lower encephalization quotients and brains that are strikingly dissimilar in structure. Studies of avian tool use could provide a wealth of information on the origins of complex tool use behavior.

Tool use in Birds

Of the approximately 21 functional and 4 manufactural categories that Beck uses to compare phyletic differences in tool behavior, he reports birds engaging in 15 (Beck, 1980, p.120-121). Some of those avian tool behaviors include well-known examples like the woodpecker finches' (*Cactospiza pallida*) use of twigs while foraging for invertebrate prey, the green herons' (*Butorides virescens*) use of bread, pelleted fish food, and even a feather as fish bait, and active anting as performed by many passerines. Lesser-known examples include the white-breasted nuthatches' (*Sitta carolinensis*) rubbing blister beetles (*Meloe angusticollis*) and other items around its nest cavities as squirrel repellent (Kilham, 1968, 1971), Egyptian vultures' (*Neophron percnopterus*) breaking open ostrich eggs either by tossing stones onto them or by hammering them with stones held in their beaks, and a nesting pair of ravens' (*Corvus corax*) dropping/throwing golf-ball sized rocks onto marauding scientists (Janes, 1976).

While many examples of avian tool use have been catalogued, almost nothing is known about the ontogeny of these behaviors. It appears that only two exceptions exist. One involves an Egyptian vulture that developed stone throwing in isolation (Thouless, Fanshawe, & Bertram, 1989). Unfortunately no follow up research has been conducted. The remaining exception, however, is truly exceptional.

Tebbich and colleagues have embarked upon a line of research dedicated to the most well-known avian tool user, the woodpecker finch (*Cactospiza*

pallida). Their research has produced, to this writer's knowledge, the only existing investigation focusing upon the ontogeny of a species-typical tool use behavior (Tebbich, Taborsky, Fessl, & Blomqvist, 2001). Tebbich et al.'s study followed tool use development in 12 wild-caught nestlings, only half of which were exposed to a tool-using model during their juvenile period. Nonetheless, all the birds developed tool use, and 5 developed a species-atypical form. For 7 birds, prey was never actually captured; nonetheless, the tool use behavior continued along the same developmental path as it did for those that did capture prey. Tebbich et al. concluded that using twigs or cactus spines while foraging for prey is "a species-typical behavior that matures," one for which improved coordination is gained during a period of "undirected playful manipulation" in which all the birds engaged at a particular stage of development. Tebbich et al. also suggested trial and error learning as the mechanism by which the motor coordination is fine tuned (see also Tebbich & Bshary, 2004). Research of this nature and calibre are key to understanding the origins of other forms of avian tool use¹⁰.

Tool Use in *Corvus*

Another notable avian tool user is the crow. The genus *Corvus* contains 47 species of crows, ravens, rooks and jackdaws. All are highly social, vocal mimics that engage in complex, adaptive behaviors such as caching, communal

¹⁰ Beck's book cited about 30 avian species engaging in tool use. Boswall further solicited and catalogued a number of reports of avian tool use, each of which he described and many of which he illustrated (Boswall, 1977, 1978, 1983a, 1983b). These records show about 25 species of birds engaging in 18 categories of tool use³. However, the most recent compilation of avian tool use reports 39 species engaging in about 38 kinds of tool use (Lefebvre, Nicolakakis, & Boire, 2002).

roosting, and kleptoparasitism. As a group they are distinguished among avian tool users by the diversity of their tool behaviors.

Table 1 (end of chapter) provides a comprehensive list of tool use reports for *Corvus*. This list shows that seven species have been observed in fifteen acts of tool use using eleven different objects. What do crows do with their tools? Perhaps not surprisingly, they mostly use them to get food.

The American Crow (*C. brachyrhynchos*) has been observed breaking open acorns by hammering them with stones held in the beak. Both the Black Crow (*C. capensis*) and the “White Necked” (Pied) Crow (*C. albus*) have been observed dropping/tossing stones onto ostrich eggs to break them open. The Fish Crow (*C. ossifragus*), Common Raven (*C. corax*), and the East African Fan-Tailed Raven (*C. rhipidurus*), have also been seen engaging in apparent food-related tool use, though no food was actually obtained. The first two instances respectively involved the dropping/tossing of marsh grass or grass tufts onto incubating Kittiwakes or gulls, presumably in attempts to harass them off their nests. The raven was seen repeatedly hammering on a ping-pong ball with a stone held in its beak; perhaps the ball appeared to the raven as an unusually hard egg. The Northwestern Crow (*C. caurinus*), New Caledonian Crow (*C. moneduloides*, discussed further below) and House Crow (*C. splendens*) have all been observed foraging for invertebrate prey while holding various kinds of sticks, twigs, or leaves in their beaks.

Not all *Corvus* tool use is food-related, though. Both the American Crow (*C. brachyrhynchos*) and Common Raven (*C. corax*) have been reported

engaging in nest-defense by dropping/tossing rocks onto intruders. Another instance of dropping/tossing involved a large flower-petal dropped by an American Crow (*C. brachyrhynchos*) onto a sibling on a lower branch. In response, the sibling flew away, but in this instance the observer said the behavior appeared playful rather than agonistic.

Two other cases of tool use involve artefactual (human-produced) objects and the containment of water. The first involved a captive Rook (*C. frugilegus*) that repeatedly inserted a drain plug into a drain near a dripping water faucet; a small pool resulted which all four Rooks in the aviary used for drinking and bathing. The final case, which will be discussed in more detail below, involved an American Crow (*C. brachyrhynchos*) using a small plastic cup to acquire and transport water. But first, studies on the one *Corvus* species that also repeatedly engages in tool modification or manufacture will be addressed (see also Caffrey, 2000 regarding an American Crow).

Tool Manufacture in the New Caledonian Crow

The New Caledonian Crow (*C. moneduloides*), an isolated Australasian species, is currently receiving much public as well as scientific attention. For the past ten years Gavin Hunt and his colleagues have been conducting field investigations during which these crows have been observed holding various types of vegetation in their bills while searching for invertebrate prey in holes and crevices. However, most remarkably, it has also been reported that they engage in the modification or manufacture of two tool types for which at least five different forms have been documented: *stick-like tools* including twigs and

hooked-twigs, and *leaf tools* including narrow leaves, wide leaves and tapered leaves (stepped-cut *Pandanus* leaves) (Hunt, 1996, 2000; Hunt, Corballis, & Gray, 2001; Hunt & Gray, 2002b).

Without a doubt, field studies of this nature are laborious to conduct, and the published accounts may not represent the full state of knowledge currently held by the researchers. However, of the seven studies published so far, relatively little of the tool manufacturing process for the more complex tool forms has actually been observed. Hunt and his colleagues have reported observing crows in the process of removing the leaf from a leaf stem to make straight twig tools “many times ... by several individuals” at Sarraméa over a 20-day sampling period, Hunt, 2000) and an unspecified number of times during a two-month data collection period involving four individual crows at Sarraméa (Rutledge & Hunt, 2004). But the making of hooked-twig tools has been seen only four times over approximately two years of observations (in Pic Ningua, Hunt, 1996), and only one individual has actually been observed making stepped-cut *Pandanus* leaf tools, though it was reported to have made 40 tools at the time of observation (Hunt & Gray, 2002a).

In a 2002 study, focusing solely upon the *Pandanus* leaf tools, Hunt & Gray reported the results of a distributed geographical study in which they collected and analyzed *Pandanus* tool counterparts (the remaining leaf from which the tool was cut) from twenty different locations on Grand Terre and one

location on Maré Island¹¹. Based on the tool characteristics inferred from the counterparts, and the observation of the one crow mentioned above, Hunt & Gray produce a plausible account of the behavioural steps a crow might go through to produce a narrow, wide or stepped-cut *Pandanus* leaf tool. The analysis of thousands of leaf tool counterparts and one bird to reconstruct a set of possible behavioural steps leading to tool production was an innovative technique which has provided a theory from which testable hypotheses may be generated. However, this population of crows also offers an unprecedented opportunity for “on the hoof” investigations of tool use behavior development, tool development, and tool production in a free-living Corvid population. Maré Island, where only wide leaf-tool counterparts have been found, and only non-hooked twig-tools have been observed in use, might be an especially fruitful location for longitudinal studies. From a behavioural standpoint, it is disappointing that these studies have not produced more direct observations of actual behavior, rather than inference about it from aftereffects. Hopefully, future reports will provide detailed accounts of the crows’ behavior during tool production.

The New Caledonian Crow in the Laboratory

Laboratory studies have also been initiated with two captive New Caledonian Crows: Abel, a male, age unknown (deceased August 2003), who lived in a New Caledonian zoo for ten years before being drafted for research in March 2000, and Betty, a female, who was taken as a juvenile from the wild, also

¹¹ Maré is an island located about 100km northeast of Grand Terre. The New Caledonian Crow was introduced there about 150 years ago (Delacour, 1966 as cited in Hunt & Gray, 2002) and have presumably remained an isolated population since then.

in March 2000. Two studies on these subjects have so far been published, both of which have employed the use of artefactual stick tools in artificial foraging situations in an attempt to address the cognitive capabilities of the species.

For one study (Chappell & Kacelnik, 2002), food was placed at varying depths inside a clear, plastic, horizontally oriented tube, which was open only on one end. The birds were presented with a vertical display of several stick tools that varied only in length (the sticks had been made by the researchers from 2mm diameter bamboo skewers). To retrieve the food, it was presumed that the birds would have to choose a stick-length appropriately matching the depth of the food. There were two versions of the task. For the first, the tube and sticks were placed side by side on a tabletop; in the second, the tube and sticks were separated by 4 meters distance and by two barriers designed to keep the crows from seeing the tube and the sticks at the same time.

Results from the first task showed that the birds chose the longest tool available on 50% of trials, and a tool matching the distance of the food on 20% of trials. This resulted in the retrieval of the food significantly more often than one would expect by chance. The researchers conclude that there was not a substantial improvement in performance across the duration of the experiment, and that the birds behaved as if using a bimodal rule of choosing either a closely matching length, or the longest tool.

The results were essentially the same for the second (visually occluded) task. The longest tool was selected on 20% of trials, and a matching tool on 15% of trials, resulting in a tool choice that was significantly better than random.

However, the results for this last task were only based on Abel's performance; Betty did not complete any of the trials within the two-hour trial-allotment. The authors assert that these results provide evidence for the rare, primarily primate, characteristic of tool selectivity, but do not comment upon the underlying cognitive processes that might be responsible.

The second study which involved only Betty, garnered much media attention (Weir, 2002). During the 5th trial of an experiment in which Betty was faced with the task of choosing an appropriate tool to solve a food-retrieval problem (there were only two choices this time, a straight and a bent piece of garden wire, and on this 5th trial Abel had absconded with the bent wire), Betty spontaneously bent the straight wire into a hooked shape and subsequently used it to retrieve the food. Once this occurred, the nature of the ongoing experiment was changed and for 17 additional trials, a single, straight piece of wire was placed atop the tube and Betty's actions were recorded. She subsequently bent the wire and retrieved the food from the tube on 9/17 of those trials.

The authors assert that (a) Betty had "little exposure to and no prior training with pliant material" except for one hour of exposure to flexible pipe cleaners about a year prior to the experiment, (b) they had never seen her "perform similar actions with either pliant or non-pliant objects", (c) she had no model to imitate, and (d) that no opportunity existed for hook-making to emerge by chance shaping. The authors conclude that Betty is capable of tool modification for a specific task.

However, once again, the authors made no attempt to address the underlying processes that might have been responsible for Betty's behavior. Nonetheless, these results generated much general speculation in the scientific community on the New Caledonian Crow's "understanding" of the hook.

Both the free-living and laboratory branches of research on the New Caledonian Crow are producing intriguing and provocative data. Nonetheless, the origin of this species' tool use remains unknown, as does the origin of its tool manufacture, though Hunt & Gray (2002) suggest that for the latter, social transmission "seems probable". Chappell & Kacelnik (2002) state that both subjects were wild caught and showed extensive use of tools upon first arriving in the laboratory aviary. Unless the animal's have a known experiential history, laboratory studies cannot address the origin of the tool use. Perhaps future research will address this topic.

The Ontogenesis of *Corvus* Tool Use

Corvus species provide a rich resource for research on tool use and its development. However, only two studies specifically addressing ontogeny have been published (Porter, 1910; Powell & Kelly, 1975, 1977).

The first, which involved captive crows in an outdoor aviary, was one of a series of ten studies investigating "intelligence and imitation" in several different bird species. The methodology involved a variant on Thorndike's puzzle-box task in which food was placed inside a small wire cage and strings were available that, when pulled, activated a latch that opened the door and allowed access to

the food located inside (Porter, 1910)¹². One adult and two hand-reared juvenile crows were used as subjects. Once the adult had learned to open the door, the two juveniles were allowed to observe its behavior and their subsequent responses were noted. Porter concluded that the young crows changed their behavior after observing the adult, and thus provided the best evidence of all the ten species in his comparative search for imitation in birds. However, crows have a strong propensity for pulling and tugging at string or string-like materials (P.D. Cole, personal observation). A more likely explanation would be that, rather than imitating the adult, the juvenile crows were drawn to different string locations through local enhancement, and once there, did what came naturally. Nonetheless, given its highly social nature, the American crow would be an excellent candidate for studies addressing social learning.

The second study involved an operant technique (Powell & Kelly, 1975, 1977; Powell, Kelly, & Santisteban, 1975). Four wild-caught adult crows were individually hand-shaped to peck a small, lighted key inside a conventional operant-conditioning chamber. Doing so provided access to a hopper full of dog food. After their keypecks became reliable, a metal grating was placed over the key so that it was no longer accessible by beak alone and matchsticks of a sufficient length to operate the key through the grating were placed on the floor of the chamber. After 50-75 hours of exposure to this task, none of the crows had

¹² Please note that Porter did not claim to have demonstrated tool use. However, it might be considered so by Beck (1980) who included crows pulling up fishing lines in his list of avian tool use. Nonetheless, given that Porter's is one of the very few studies to address the possible transmission mechanisms underlying object-directed behavior of crows, it seemed fitting to include it here.

spontaneously used the matchsticks to extend their beak-reach and operate the key.

The researchers subsequently trained two of the four crows to use the matchstick by shaping their behavior through reinforcing successive behavioral approximations. The remaining two crows did not respond to shaping and were instead trained through a fairly complicated method involving the positional fading of a T-bar. Once the tool use was reliably established by these methods, the crows readily generalized their learned stick-poking behavior to other objects such as paper clips, nails, and wooden sticks.

The crows then surprised the researchers by modifying their tool use behavior into an ostensibly more efficient form. They began to persistently wedge the tool between the edge of the response panel and the key, so that it could be acted upon as a lever rather than a beak extension. The authors concluded that the wedging and levering were “innovative” behaviors. However, elements of stick-probing behavior might be innate in origin. Probing or poking with stick-shaped objects into crevices has been reported in the New Caledonian Crow (*Corvus moneduloides*), the Northwestern Crow (*Corvus caurinus*, Jewett, 1924), as well as the American Crow (*Corvus brachyrhynchos*, Caffrey, 2000) in foraging contexts, and spontaneously appeared at a very young age in an American Crow hand-raised by the author (P.D. Cole, unpublished data).

The crows in Powell and Kelly’s study, which were housed and worked individually, could have, after being trained to use the stick as a beak extension, begun to actively stick-forage in the crevices around the key area. In doing so,

the tool could have become tightly wedged, at which point even the slightest pressure on it would have operated the hopper, thereby reinforcing the crows' probing and levering behavior. Powell and Kelly more correctly conclude that the crows' tool use demonstrates how "seemingly complex behaviors can be built up through the operation of relatively simple conditioning procedures".

As promised, one last report remains to be discussed. It involves a rare form of animal tool use, irrespective of species ^{13, 14}, and occurred in a captive crow housed at the Allee Laboratory of Animal Behavior at the University of Chicago in the mid 1960's.

It was reported that, on days when the caretakers failed to do so, the crow would fill a small plastic cup with water by dipping it into its water trough, carry it up to 5m, and finally pour it over its dry food ¹⁵. The behavior was reported to have appeared spontaneously, with no training or shaping. This is indisputably tool use, clearly resourceful, and novel for the individual, species and genus, and it provides suggestive evidence for imitative learning. Such cross-class imitation might seem far-fetched, but occurs in imprinted individuals (e.g., Moore, 1992).

Beck's report doesn't specify if the crow in question was human-imprinted. It also

¹³ Beck (1980) and Boswell both cite the same psittacine examples of an African Grey Parrot (using a briar pipe), lesser sulphur-crested cockatoo (nutshells), a cockatoo of unknown species (half walnut shell), and keas (cans and cups) baling water from containers, though only the lesser sulphur-crested cockatoo actually drank the acquired water. However, in all of these cases the birds were captive, their histories unknown, and imitation a probable contributor.

¹⁴ Antevs reported a wild male gila woodpecker (*Centurus uropygialis*) dipping bits of bark into a thinned honey solution, which he then fed to fledglings (1948). It is not clear if the feeding of bark bits to fledglings is normal for this species, and since similar behavior has not been seen again, it is possible that this bird stopped to consume the solution and put the bark down in it order to do so.

¹⁵ This report initially came in the form of a personal communication from E. Hess to Beck in 1965. The crow's behavior was subsequently personally observed by Beck in 1965.

doesn't specify whether the caretakers moistened the crow's food in the same manner as that used by the crow. If not, then this tool use act could represent a truly innovative development, rather than evidence for imitation. Either way, it is an exceptionally intriguing case, and it is unfortunate that the development of this rare form of tool use was not documented.

Of the existing studies on tool use in *Corvus*, none has directly addressed ontogeny. Determining the origins of a tool use act, in any but the simplest case, can be a daunting laboratory task requiring an understanding of the principles of learning, absolute environmental control, and thorough knowledge of species-typical behavior. The purpose of the research conducted for this dissertation was to trace tool use ontogenesis in an individual belonging to a species recognized as accomplished and resourceful tool users. Given their reputation and local abundance, the American Crow (*C. brachyrhynchos*) seemed a promising species with which to undertake a series of studies. The challenge would be to determine if and to what extent innate and species-typical behaviors played a role, what kinds of learning, social or asocial, might be involved, and whether complex cognition appeared necessary, in the development of specific tool use acts.

Table 1. Tool Use in *Corvus*: Crows, Ravens, Rooks & Jackdaws

Food Related: using an object as a projectile (tossing, dropping or throwing)	*	<i>Corvus</i> Species	Reference
Stone Dropping stones from a height onto Ostrich eggs	F	"Black Crow" probably <i>C. capensis</i>	De Mostenthal & Hartling (1877) as cited in Brooke, 1979
	F	"White Necked Crow" probably Pied Crow <i>C. albus</i>	Martin, A. (1890, as cited in Brooke, 1979)
Food Related: holding an object in the beak and hammering with it	*	<i>Corvus</i> Species	Reference
Stone "Each held under its foot a nut of the scarlet oak <i>Quercus rubra</i> and then reached for a stone which was then used as a hammer to smash the acorn"	F	American Crow <i>C. brachyrhynchos</i>	Boswall 1978 (reports a pers. com. from Duvall 1978)
	C	American Crow <i>C. brachyrhynchos</i>	
Food Related: holding an object in the beak and using it to pry/ poke/pobe into an unreachable place	*	<i>Corvus</i> Species	Reference
Sticks, Twigs & Leaves Prying/levering a peanut out of a crack in a bamboo perch using a stick	C	Northwestern Crow <i>C. caurinus</i>	Jewett 1924 (pers. com. from A. King)
Poking with vigorous head bobbing while holding a "slender twig" in the beak under bark or in the end of hollow branch	F	New Caledonian Crow <i>C. moneduloides</i>	(Orenstein, 1976)
Holding "hooked twig" in beak and engaging in both rapid (presumably prey invisible) and slow (presumably prey visible) poking of the hooked end into holes, leaf bases, and under detritus to acquire invertebrate prey	F	New Caledonian Crow <i>C. moneduloides</i>	Hunt 1996
Holding "stepped-cut" leaf (<i>Pandanus</i> sp.) in beak and engaging in rapid (presumably prey invisible) and slow (presumably prey visible) poking of the tapered end into holes, leaf bases, and under detritus to acquire invertebrate prey	F	New Caledonian Crow <i>C. moneduloides</i>	Hunt 1996

Holding leaf petiole in beak while poking into natural and artificial holes for invertebrate prey	F	New Caledonian Crow <i>C. moneduloides</i>	Hunt 2000
"Fishing" for ants with leaves	F	House Crow <i>C. splendens</i>	(Rajan & Balasubramanian, 1989)
Food Related	*	Corvus Species	Reference
Hollow Vessels Acquiring and transporting water in a small plastic cup which was poured onto dry mash (food)	L	American Crow <i>C. brachyrhynchos</i>	Boswall 1980 (pers. com. E. Hess 1965, and pers. obs. 1966)
Presumed Food Related	*	Corvus Species	Reference
Probing into a suspected arachnid hole in a wooden fence using a shard taken from the fence and modifying it by tapering one end by hammering it with the beak	F	American Crow <i>C. brachyrhynchos</i>	Caffrey 2000
Holding a stone in the beak and hammering a ping pong ball ("false egg")	F	East African Fan-tailed Raven <i>C. rhipidurus</i>	Andersson 1989
Dropping marsh grass onto incubating gulls	F	Fish Crow <i>C. ossifragus</i>	Montevocchi 1978
Dropping grass tuft onto incubating Kittiwake	F	Common Raven <i>C. corax</i>	Montevocchi 1978
Not Food Related	*	Corvus Species	Reference
Nest Defense Dropping/tossing pine cones from a height onto invading humans	F	American Crow <i>C. brachyrhynchos</i>	Caffrey 2001
Dropping/tossing stones from a height onto invading humans	F	Common Raven <i>C. corax</i>	Janes 1976
Play Acquiring and then dropping flower petal onto sibling	F	American Crow <i>C. brachyrhynchos</i>	Caffrey 2001
Drinking & Bathing Inserting a plug into a plug hole in the aviary floor so that a pool of water formed, which was used by all 4 rooks for drinking and bathing	C	Rook <i>Corvus frugilegus</i>	Reid 1982
* Field Study / Captive Housing / Laboratory Housing			

Chapter 2

A Test for Mimetic and Imitative Learning in an American Crow

(*Corvus brachyrhynchos*)

The ability to imitate movement is a complex, though poorly understood, form of learning. It can be defined as the copying of a novel or improbable act for which there is no instinctive tendency (Thorpe, 1963) and for which no simpler explanation can be found (Thorndike, 1898). In mammals, it is known to exist unequivocally only in Great Apes (gorillas, chimpanzees, orangutans and humans), though it is likely present in some cetacean species as well. In 1992 Moore published the first experimental evidence for movement imitation in a bird.

A locally purchased Congo African Grey Parrot (*Psittacus erithacus*), subsequently named Okíchoro, was the subject of Moore's five-year study. The bird was housed alone in a room within a larger laboratory. Moore entered the room several times a day, for 3 – 10 minutes, and repeatedly performed stereotyped movements, accompanied by a labeling word or phrase. Okíchoro's ensuing movement imitation was remarkable. It consisted of fourteen distinct reactions, involving a foot, the beak, the head, or the whole body, which were accompanied by vocally mimicked labels or phrases that served as declarative tags for the bird's behavior (Moore, 1992). There are 360 known species of parrots worldwide (81 genera), and whether or not other parrot species show the same propensity for movement imitation is yet to be seen.

Another group of birds, the songbirds or oscine passerines, is by far the most abundant order with 5,752 known species (1,165 genera), (Sibley &

Monroe, 1990, 1993). It is possible that some passerine species might have also evolved this adaptive form of learning. Within the oscine passeriforme order the genus *Corvus* (crows, ravens, jackdaws and rooks) encompasses 47 species. All are highly social, vocal mimics that engage in complex behaviors. One member of that group, *Corvus brachyrhynchos*, the Common or American Crow, is singular among all passerines in the sheer quantity and diversity of published acts of tool use (see Table 1, Chapter 1). It is unclear what role movement imitation might play in avian life. In primates, it appears to serve a role in the using or making of tools (Beck, 1974). However, Okíchoro's imitation never incorporated objects and appeared instead to be related to display behavior (Moore, 1996). Parrots are not generally known to be tool users – certainly not to the same extent as crows. Given that crows are such prolific tool users it may be that, at least for these particular birds, as for primates, imitation plays a role in how tool use is learned.

There is yet another reason to think that crows might be imitative learners; they are vocal mimics. While the ability to reproduce sounds may seem to have little in common with the ability to reproduce movement, Moore described a possible evolutionary path by which movement imitation might have evolved in psittacine birds with vocal mimicry as an essential prerequisite (Moore, 1992, 1996):

Song/Call Learning →

Vocal Mimicry →

Percussive Mimicry →

Visual Movement Imitation

This path necessarily predicts that movement imitation will be found *only* in a subset of birds that are vocal and percussive mimics¹⁶. But learning how to manipulate objects imitatively might be an even more complex kind of learning than movement imitation, and it is one that Moore did not include in his progression. Moore noted that when Okichoro imitated movement that had been modeled with objects (e.g., a peanut), he imitated the movements only, without incorporating the objects. This same imitative movement-only behavior was also found in a different study with a second Congo African Grey Parrot (unpublished data, P.D. Cole). Finding evidence for movement imitation involving objects in any avian species would add another tier to Moore's evolutionary progression:

Song/Call Learning →

Vocal Mimicry →

Percussive Mimicry →

Visual Movement Imitation →

Visual Movement Imitation Incorporating Objects

Given their reputation as social, vocally mimetic, tool users, the American Crow would seem to be a promising, non-psittacine, species in which to look for movement imitation, and for movement imitation incorporating objects.

A replication and extension of Moore's parrot procedure with a crow could potentially accomplish several things. If the crow proved capable of movement

¹⁶ Moore (1996) postulated the existence of percussive mimicry as an intermediate form of learning that might necessarily exist between vocal mimicry and movement imitation. He defined it as "a process in which movements are used to copy percussive sounds".

imitation, it would be the first evidence for this particular species (see the criticisms of Porter's, 1910, study in Chapter 1). If percussive mimicry was found, it would be the first evidence for this particular ability in *any* species. If movement imitation appeared without percussive mimicry, it would imply either that percussive mimicry was not an essential evolutionary step to avian movement imitation as Moore theorized, or that crows, and therefore perhaps other passerines as well, arrived at movement imitation via a different evolutionary path than psittacine birds. Finally, by adding an additional test for movement imitation incorporating objects, evidence for the existence of this ability, as well as its potential placement in Moore's theoretical pathway, could be sought.

Method

Subject, Housing and Diet

The subject of this study was an American Crow (*Corvus brachyrhynchos*) acquired on June 25, 1998 from a wildlife rehabilitator in Lake Echo, Nova Scotia. The bird was an abandoned nestling estimated to be approximately 3 weeks old at the time of acquisition. He was DNA sexed by Avigene, Inc., determined to be male, and named Loki. Hand-feeding and weaning were carried out by the Experimenter in a manner consistent with the rearing of altricial birds as companions (to encourage social bonding). See Appendix A for a timetable of events.

Loki lived and all data were collected in a 5 x 4 meter animal colony room located in the Psychology Department at Dalhousie University. The room was modified somewhat to serve as an aviary. Part of the room, where the sink, countertop, and electrical outlets were located, was sectioned off with a removable puckboard wall and Loki was allowed free-flight access at all times to the remainder of the room. Lighting was maintained on a 12/12 L/D cycle and provided by four-foot full-spectrum tubes mounted overhead. A natural tree-branch perch, food bowls, a small rock, a large plastic dog den, a blue molded plastic chair and a stainless steel pan (101cmL x 67cmW x 5cmD) were also present in the aviary. A schematic (not to scale) of the aviary can be seen in Figure 2.1.

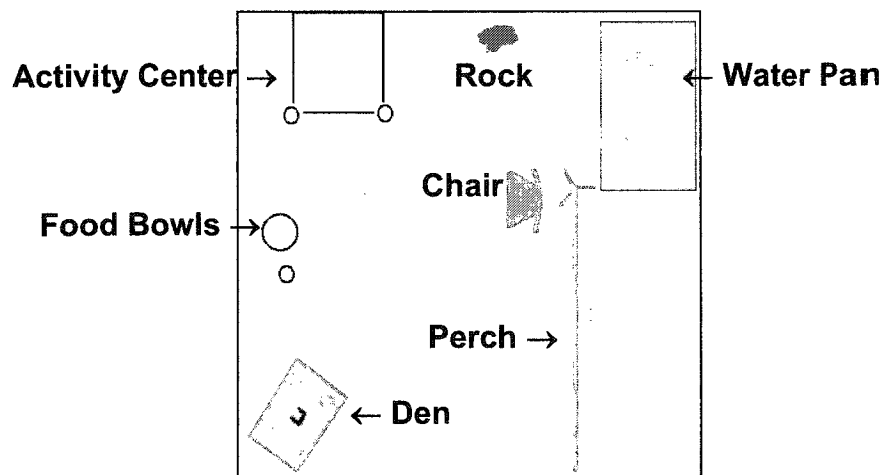


Figure 2.1 A schematic of the aviary layout for Experiment 1 (not to scale).

Once weaned, Loki's base diet consisted of Eukanuba small breed puppy chow and Pro-Plan dog biscuits. These base diet foods were always provided in

a round, 20cm diameter, stainless steel bowl located on the floor. Supplemental foods such as fresh fruits, vegetables, dry pasta, canned tuna, mealworms and cheese were also provided daily, either in the large bowl with the dry chow, or in a smaller 9cm diameter stainless steel bowl placed on the floor near the larger bowl, or placed loose on top of the den.

Human Interaction

Once Loki arrived in the laboratory and before Experiment 1 began only “Hello” was spoken in his presence. It was used as a greeting and spoken repeatedly by the Experimenter during each visit. Fourteen days after the Experimenter began modeling “Hello,” Loki began producing two-syllable utterances with Eh-O vowel sounds, and approximately one month later, he produced several intelligible “Hello” vocalizations. Once it became apparent that he was capable of vocal mimicry, it was time to begin testing. So, a week later, at which time he would have been approximately 68 days old - an age at which his wild counterparts would be learning to forage on their own and forming social alliances - Experiment 1 began.

Apparatus

Modeling was concentrated around an activity center located in the back left corner of the room (see Figure 2.2).

The center consisted of a 1.5 meter square piece of white puckboard mounted flush against the back wall of the aviary, onto which a U-shaped perch,

made of PVC tubing and hardwood dowels, was attached. Ten-cm round Tupperware containers were mounted at the two corners of the front perch. The left cup was designated as the source cup (S-cup), and the right one was designated as the receiving cup (R-cup). Twenty blue poker chip sized pieces

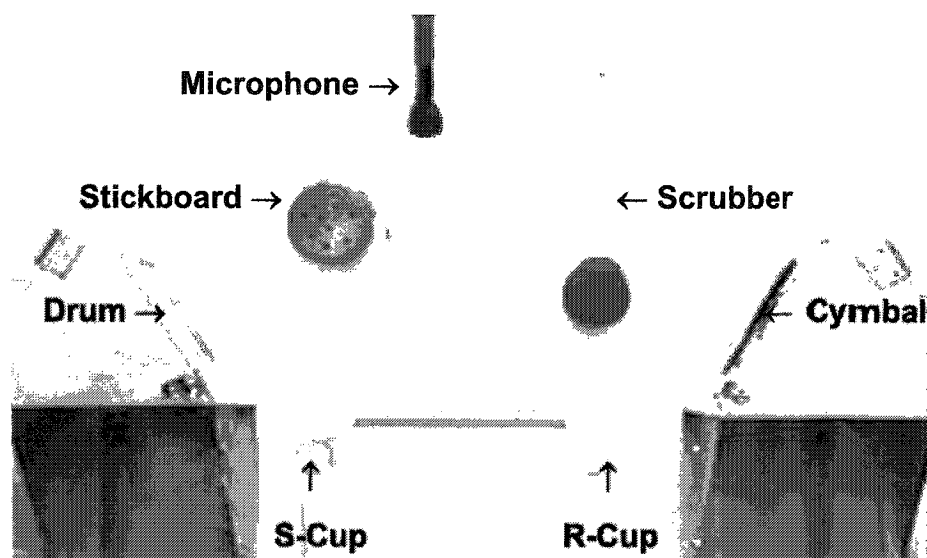


Figure 2.2 The activity center around which modeling was concentrated

of ¼ inch puckboard were located inside the S-cup. A stickboard was centered and mounted 15-cm above the left perch. It consisted of a round piece of hardwood with drilled holes, and a length of small wooden dowel tethered nearby. A tethered red plastic dish scrubber was centered and located 8 cm above the right perch. A triangular aluminum case, in which a drum practice-pad was mounted, stood outside the left side of the "U". A second identical aluminum case, in which a 30cm diameter Sabian cymbal was mounted, stood outside the right side of the "U". These cases allowed Loki access to the drum and cymbal surfaces from the perches of the activity center. Latched doors at the ends of the

cases allowed the Experimenter to access, unseen, the back of the drum or cymbal surface by opening the door and placing a hand inside the case. The scrubber and the cymbal were not used during the two Blocks of the experiment.

A Sony cassette Walkman, with a single earphone, was worn by the Experimenter during modeling sessions. It played a cassette tape that consisted of 15 sets of tones, which corresponded to the 15 sets of actions that would be modeled during each session. Each set of tones included 20 clusters of tones (to coincide with the 20 repetitions of the action within a set). Each cluster began with a distinctive set of three short tones lasting for 1 second. This was followed by seven short tones lasting 3 seconds in total, followed by a 2 second silent period. Each cluster served as a timing mechanism by which the Experimenter synchronized the associated movement. This was done to ensure that each repetition of an action spanned the same amount of time, at least as much as humanly possible.

A Panasonic VHS camcorder was mounted on a tripod and located outside the free-flight area in front of a small window. Its lens was focused on the activity center. A sound-activation unit, developed by Dr. Bruce Moore and Gordon Troop, controlled the recording function of the camera.

The audio and video outputs from the camcorder were split and routed to two television monitors located in adjoining rooms in which either the Experimenter and/or an additional observer spent the majority of each day and evening. This allowed observers to visually monitor the activity center and to hear any sounds occurring in the aviary in real time. It also provided a way to

monitor the camcorder's performance by relaying the information from its viewfinder (such as whether or not the record function was currently activated and when the videotape was nearing its end) to the monitors.

Actions and Labels

The modeled actions were considered to be of three types: movement, movement with object, and percussive. "Movement" actions were defined as physical behaviors of which crows were believed to be capable, but which are not a part of their natural behavioral repertoire. "Movement with object" met the same criteria but incorporated an inanimate object. For "percussive" actions, the Experimenter tapped a four-beat rhythm on the drum with the action hand hidden inside the case. Thus Loki would *hear* the sound without seeing *how* it was produced.

The experiment was conducted in two Blocks, with one exemplar of each of the three types of actions modeled in each Block, resulting in a total of six actions for the entire experiment. Each action was preceded by a distinctive verbal label which was spoken just prior to its modeling. For example "bend bend" was spoken each time just prior to executing a bending motion from the waist. It was hoped that Loki would learn to vocally mimic the label as well as reproduce a recognizable approximation of the associated action. By reproducing the label Loki would (a) trigger the sound activation unit to turn on the camcorder and (b) announce the movement he was about to perform. See Table 2 for a listing of labels and their associated tasks.

Table 2. Verbal Labels and Associated Actions used in Experiment 1

Block 1	Label	Action
<u>Movement</u>	Bend Bend	Sideways bending motion from the waist always first left and then right
<u>Movement w/Object</u>	Stick Stick	Using right hand, tethered stick is inserted into one of 10 available holes in a round piece of wood
<u>Percussive (Drum)</u>	Two Two	X XX X
Block 2		
<u>Movement</u>	Rap Rap	Left arm up, elbow bent, hand fisted and rapped forward three times
<u>Movement w/Object</u>	Move Move	One poker chip is moved from S-cup to R-cup
<u>Percussive (Drum)</u>	Eight Eight	X X X X

Procedure

One week of baseline data were collected before the experiment began. Each morning the Experimenter entered the room and made notes regarding the location of all moveable objects. The objects were then placed back in their starting locations, and the aviary and its contents were hosed down with warm, soapy water. Finally fresh food and water were provided and the Experimenter left the aviary. Once the experiment began, there was always at least ½ hour gap between the end of cleaning and the beginning of a modeling session (all modeling was performed by the Experimenter).

The experiment itself consisted of two 15-week Blocks. Each Block included 13 weeks of modeling and data collection, followed by a two-week period during which no modeling occurred but data were still collected. During Blocks, modeling sessions were conducted twice a day, 5 days a week, in the morning and late afternoon, with a minimum of 5 hours between a morning and afternoon session.

For each session the Experimenter modeled a particular action 100 times in total. However, these repetitions were broken down into 5 separate sets of 20 repetitions each. The order of sets was randomized before every session. For example, a Block 1 session consisted of 5 sets (20 repetitions each) of “bend bend”, 5 sets of “stick stick”, and 5 sets of “two two”, resulting in a total of 15 action sets per session. The order in which the 15 sets were modeled was randomized before each session. By the end of a Block, the experimenter had modeled each action 13,000 times.

Data Collection

The Camcorder monitored the activity center area constantly. Loki's behavior usually resulted in activating the camcorder often enough that one videotape per day was produced (two hours). However, occasionally on very active days, two tapes per day were produced. Videotapes were collected from the camcorder once daily, during the morning aviary cleaning routine, and on active days again shortly before the evening modeling session. The Experimenter reviewed the videotapes daily.

Evidence for movement imitation, imitation with object and percussive mimicry was sought by visually scanning the videotape in fast forward for any action that occurred at the activity center. Once Loki was seen in the frame, the tape was returned to normal viewing speed and, simply put, any behavior that seemed out of the ordinary was noted and archived onto another videotape. All interactions with objects at the activity center were also noted and archived. Any such behavior had the potential to be an early developmental stage of movement imitation.

Evidence for vocal mimicry was sought primarily through real-time observation. Whenever a vocalization was heard that seemed mimetic, the videotape for that day was reviewed in its entirety at normal speed, and the prior day's as well, and so on until a 24-hour period had passed in which the vocalization was not heard. Vocal mimicry, especially in younger birds, does not always manifest with high fidelity upon first attempt. In Psittacines as well as Passerines, a mimicked English word or phrase usually goes through an initial stage in which only the vowel sounds are reproduced, to which the beginning and ending consonants are added later (P.D. Cole, unpublished data). To represent these stages developmentally, Loki's vocal mimicry was rated on a qualitative scale that recognized three levels of intelligibility. A vocalization was rated "C" if only the person who had modeled it recognized it, "B" if strangers could recognize it with some coaching, and "A" if strangers could recognize it without coaching.

Results

Baseline

One week of baseline data for the activity center were collected. During and prior to that time, Loki was not observed engaging in any behavior that resembled a sideways bending motion, or a rapping motion with either leg. He did not interact with the stick or scrubber at all. However, he did transfer poker chips from the S-cup to the R-cup four times. Transfers occurred along with much additional fiddling with the chips and the cups. Chips were also transferred in the opposite direction three times. But mostly, they were tossed to the floor, or carried away in the beak. He also tapped, pecked and scraped his beak across the drum on seven separate occasions.

Experiment

Vocal Mimicry

Loki continued throughout the experiment to mimic “Hello”, and also produced vocalizations that sounded like laughter. However, he vocally mimicked only one of the six experimental labels. Early renditions of “rap rap” were heard 78 days after first exposure, though it only reached “B” level clarity. In general, humans unfamiliar with the label said that it “sounded like English” but they could not correctly identify the words without coaching.

Percussive Mimicry

While alone, Loki often pecked the drum forcefully with his beak (the drumhead had to be replaced twice during the experiment). However, the

tapping never approximated the modeled rhythms enough to warrant further analysis. He often tucked chips, feathers and food bits between the drum and its frame. He also occasionally pecked the cymbal, but most often just placed food, feathers or other loose objects against the cymbal and then pressed them downward, thereby depositing them inside the cymbal casing. No evidence for percussive mimicry was found.

Movement Imitation and Movement Imitation with Objects

Loki never produced any approximation of the bending or rapping movements the Experimenter modeled so exhaustively.

He removed the stick from its tether so often during Block 1 that remounting became futile, and it was eventually left off the tether altogether. When the Experimenter went into the aviary to model, the stick had to be located. It was then placed inside the pocket of the lab coat worn by the Experimenter and retrieved when needed for modeling. At the end of the session it was left lying on top of the stickboard. Loki was often seen pressing the stick flatly against the stickboard with it held parallel in his beak, but he never placed the stick *into* the holes. He did however occasionally fill the holes with bits of wet chow.

Even though the scrubber was not used as an experimental object, Loki began interacting with it two days after the experiment began. He would grasp it in his beak and pull at it or press it to the puckboard backing. Approximately one

month later, he had learned how to remove it from its plastic holder. After that, it required near daily reattachment.

Loki moved poker chips from the S-cup to the R-cup on nine occasions during the entire span of the experiment (6 times during Block I, and 3 times during Block II). However, he tossed or took chips from the S-cup, and placed them in the bath, the bowl or in other areas around the aviary every day. Once again, prior to each modeling session the Experimenter had to locate the chips and place them back in the S-cup. While Loki usually left them alone during the modeling session, he would toss or take them out of the cup almost immediately after the Experimenter left the aviary. Food, feathers and the stick were all placed in the S- and R-cups with greater frequency than the chips. No evidence of movement imitation, with or without objects, was found.

Conclusions

After nine months of videotaped data collection, and another three months of real-time monitoring, no evidence for movement imitation with or without objects, or for percussive mimicry, was found - certainly nothing comparable to that seen in Okíchoro's behavior. Accordingly, this study did not provide justification for additional tiers in, or a reordering of, Moore's theoretical account of evolutionary development of avian movement imitation. Further research will be required to determine if any passerine is capable of movement imitation with or without objects, and whether percussive mimicry actually does exist in any

avian species. Nonetheless, this study did produce several other behaviors that warrant mentioning.

Social Bonding and Stimulus Enhancement

Social bonding was evident. Loki often greeted the Experimenter with juvenile food-begging behavior (wing-quivers, distinctive species-typical vocalizations) and later, as he matured, with drooping wings, bowing and “Hello”. He almost always came to the activity center while the Experimenter was modeling. Usually he sat on top of the drum or cymbal casing, and oriented to the Experimenter’s hands (during object manipulation or gesturing), or body (in the case of the bending action). When the Experimenter entered the room for other reasons, such as cleaning or camcorder maintenance, Loki either followed along behind or sat and watched the activity. He often solicited head scratches, which were always granted except during modeling sessions, by closely approaching the Experimenter and bowing his head.

After the Experimenter manipulated some object in the aviary, such as reattaching the scrubber, Loki would approach and manipulate that object, though he usually waited until the Experimenter had left the aviary before doing so. His social bonding with the Experimenter was undeniable and should have provided a strong incentive for movement imitation but resulted only in vocal mimicry and stimulus enhancement instead.

Caching and Soaking

Loose objects (food, feathers, nuts, bolts, scrubber, stick, poker chips) were often tucked underneath the PVC tubing that formed the frame for the removable puckboard wall that formed one side of the aviary, placed inside the cymbal case or, most often, in the bath or bowl. Objects placed in the bowl were often pushed deeply underneath the chow, as if they were being hidden or cached. Additionally, every day food or food remnants, as well as non-food objects, were found in the bath. These caching and soaking behaviors began very early, with the rudiments appearing only ten days after Loki's arrival, when he was approximately one month old.

Object Manipulation

Many fixed objects were manipulated until they became mobile. This included experimental (stick, scrubber) as well as non-experimental (floor molding, plastic cable ties) fixtures. Loki learned to unscrew the wing nuts and bolts that held the dog den together. He quickly learned (within the baseline period) how to open the simple locking mechanism located on both the drum and cymbal casings. After doing so, he would often grip the lock in his beak and use it to repeatedly bang the casing doors open and shut. In short, Loki repeatedly manipulated *every object* within reach, though not in imitative ways.

As stated before, there were differences, aside from the species, between this procedure and Moore's (1992). Perhaps procedural disparities can be held

accountable for the lack of imitation. The most obvious and, also perhaps the most important, differences involved the structured nature of the modeling procedure, and the overall length of the study.

In Moore's study, modeling visits were conducted "for 3 -10 minutes several times daily" and movements were "stereotyped". However, it is unclear from the published report just how many times a day each particular action was modeled, and/or if all actions were modeled every day (Moore, 1992). In the current study, actions were repeated numerous times within a session (100 repetitions), the sessions were longer (about an hour), and occurred less frequently (twice a day). Actions were also synchronized with a timing device to decrease inter-repetition variability. These changes obviously introduced much more structure into the modeling procedure. More structure would seem to be an advantage. However, such rigid structure may not create a favorable environment for avian imitative learning. It is colloquially reported that mimetic parrots are unlikely to learn new words or phrases via sheer repetition. However, a single dramatic word or phrase (usually unintended and often containing expletives) can be learned after only a single hearing. While vocal mimicry and movement imitation are not the same learning process, this study presupposes that they are related processes, which means they might be subject to the same constraints. This is not to say that repetitive behaviors are not imitated, for certainly they were in Okíchoro's case. However, Moore's modeled behaviors might have been made more socially pertinent merely by their relatively infrequent nature. Perhaps the procedure used here was simply *too*

structured, and the exhaustively modeled behaviors, rather than acquiring salience through repetition, became socially irrelevant.

Moore's study lasted for five years, while this study attempted to find imitation in only a year. However, at the time of this writing, Loki is 6 years old, and has been under constant observation. Nearly every day of his life, he has witnessed human behavior and/or had human social interaction; either with the human to whom he is bonded, three other eventually familiar humans, or the occasional stranger. After this study ended, a semi-circular right-arm wave was implemented as a departing gesture, and has since been used by all human visitors. It was accompanied by the words "so long". Other behaviors have been informally modeled during the daily aviary cleaning and several other recurrent procedures. Nonetheless, over the additional five years of repeated exposure to the stereotyped wave, and many other human behaviors, Loki has never shown even the slightest hint of movement imitation.

Negative results with a single subject can never answer the question of whether or not crows are capable of movement imitation. However, a complete dearth of imitative behavior, in the face of the fact that this particular subject was (a) such an ideal candidate in so many other ways, and was (b) persistently and longitudinally exposed to scores of potential source behaviors, compels the conclusion that movement imitation and, perhaps therefore, movement imitation incorporating objects, is not likely a component in the learning repertoire of the American Crow.

Chapter 3

Spontaneous Tool Use

Even though Loki did not exhibit imitative behavior involving objects, he did engage in tool use. This chapter describes six instances of tool use involving four different objects. For most instances supplementary digital video (denoted by DV1, DV2, etc.) has been provided in Appendix D.

Observation 1: The mobile perch as ladder

Loki's first act of tool use occurred during Experiment 1. Two objects were involved, a mobile perch (a lightweight, metal tripod with a wooden dowel attached, see Appendix B, Figure B1) which was usually tucked under the front PVC perch of the activity center (Chapter 2, Figure 2.2), and the microphone that hung above the activity center. At the time of this incident, the microphone was in its second location. In its first location, it was about 30cm above, and 30cm in front of, the foremost activity center perch. This was too close to the perch and Loki pecked and pulled at it repeatedly. To prevent damage, the microphone was relocated, higher above (about 45cm) and farther out in front of the perch (about 60cm) where Loki was not able to reach it. But he still tried. He frequently flew up to it, grasped it with his feet, and pecked at it - but he always slipped off within seconds. It was assumed that this behavior would simply extinguish.

However, shortly before the end of Block II modeling (on Feb 3, 1999), the videotape revealed the mobile perch moving in small, jerky increments, from its original location near the activity center perch, across the aviary floor until it was

positioned underneath the microphone. Then Loki boarded the perch and began to peck energetically at the microphone (see Figure 3.1).

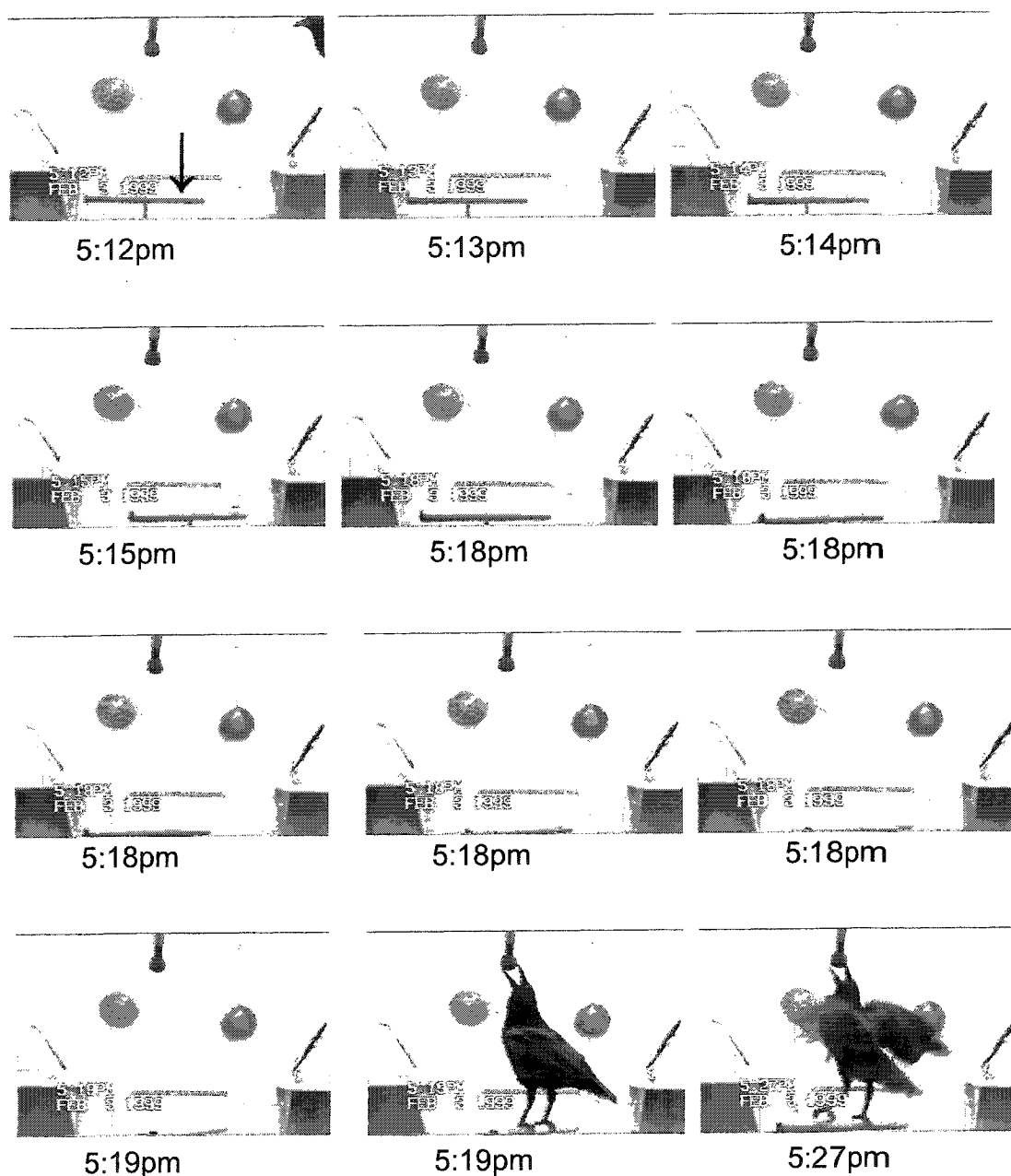


Figure 3.1 A sequence of still-frames taken from video showing the upper part of the mobile perch (indicated with an arrow in the 5:12pm frame) moving across the aviary floor until it was positioned underneath the microphone. Then Loki boarded the perch and began a sustained bout of pecking at the microphone (see also DV1, Appendix D).

Loki had moved the perch at least 60cm, though the perch did not travel in a direct path, so the distance was likely a bit more. The mobile perch was removed from the aviary the next day, Experiment 1 continued, and the microphone-directed behaviors did finally extinguish.

About seven months passed between the time Loki first had access to the mobile perch and when he moved underneath the microphone.

Observation 2: The Frisbee as scoop and platter

From very early on, Loki carried food in his beak to the bath where it was deposited and either eaten immediately or left to soak and consumed later. Wild crows are known to do the same with pieces of bread or dog food, using puddles and backyard birdbaths. So finding chow and other food bits floating in Loki's bath was a common occurrence and did not arouse any suspicion. However, in late December of 1999, the food in Loki's *bowl* was found to be wet.

A color Hitachi CCTV camera, model VK-C360N, and an Electrovoice microphone were centrally mounted on the aviary ceiling. The camera provided an overhead view of the entire aviary. It revealed Loki making trips to and from bath and bowl while carrying a small Frisbee in his beak. It appeared that the Frisbee, which had been provided as a novelty object for environmental enrichment about six months earlier (see Figure 3.3, and Appendix A for introductory dates of this and other objects), was being used to take water to the bowl.

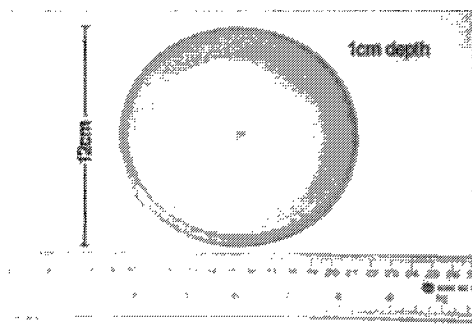


Figure 3.3 The Frisbee.

A fourteen-day observation period was conducted to determine the rate at which the Frisbee was being carried to either bath or bowl, and whether or not it was introducing water into the bowl. The camera and microphone outputs were routed to a JVC time-lapse video recorder located in a separate room. The aviary was continually videotaped, in time-lapse mode (3 frames per second).

Diet was the same as in Experiment 1. Housing was also the same as in Experiment 1, with the following exceptions. The activity centre had been removed and a second stainless steel pan, identical to the first (101cmLx67cmWx5cmD), had been placed in its stead. This new pan now served as the bath pan, and the other pan was left empty (dry). A second medium sized rock was also added near the bath (see Figure 3.4 for the aviary layout). Enrichment objects, aside from the Frisbee, that were present in the aviary at the time of this data collection included three poker chips left in the aviary after Experiment 1, two orange molded plastic shapes (a square and a circle) taken from a chewable parrot toy, a small, yellow, plastic bead, a keychain (a quick-link with one key and a few short lengths of stainless steel chain), a grey

plastic spool, a multicoloured plastic Slinky, and a white plastic practice golf ball (see Appendix A for a timeline and Appendix B for photographs).

The Experimenter cleaned the aviary each day around noon. After cleaning, all aviary appointments were placed back in their original locations, and enrichment objects were left on the floor near the den in the “toy corner”.

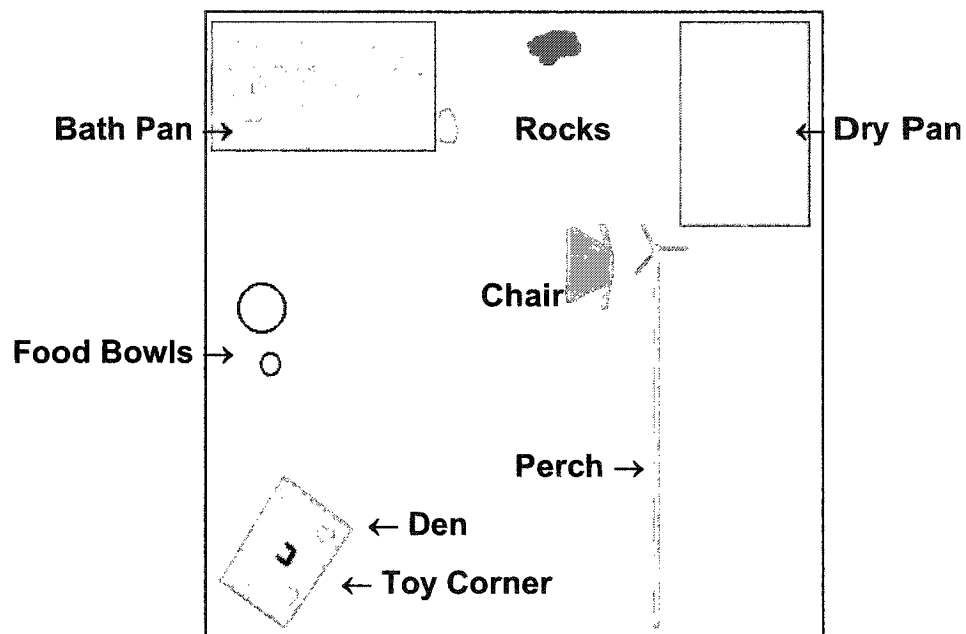


Figure 3.4 A schematic of the aviary layout during Observations 2, 3 and 4 (not to scale).

The videotapes were reviewed to determine the frequency with which the crow carried the Frisbee in a direct path either from the bath to the bowl, or from the bowl to the bath. These were scored as “direct trips”. Whether the chow in the bowl appeared moist was noted once daily (at midday) when the Experimenter cleaned the aviary and replaced the food.

Bath-to-Bowl Trips

Direct trips from bath to bowl occurred on 10 out of 14 days, with a total of 30 direct trips documented. The height from which the camera viewed the aviary made it difficult to determine if the Frisbee always held water on these trips. However, on many occasions, water was unmistakably seen spilling from the Frisbee as it was carried towards the bowl, and the daily visual inspection found indications of water accumulation in the bowl on 9 out of 14 days.

Bowl-to-Bath Trips

Direct trips in the opposite direction, from bowl to bath, also occurred on 10 out of 14 days, with a total of 29 direct trips documented. In contrast to the water, food was clearly visible in the Frisbee on every bowl-to-bath trip. Thus it became apparent that Loki was also transporting food to the bath with the Frisbee.

After these data were collected, a Sony camcorder (model TR940) was mounted on the wall directly above the food bowl and the focus zoomed to show only the bowl or the bath and a small area of the aviary floor around it. Figures 3.5, 3.6 and 3.7 were taken from these videos. These videos also revealed Loki loading novelty objects from the bowl onto the Frisbee (using his beak) and carrying them away.

Over about three months, Loki was seen repeatedly using the Frisbee to transport objects, and to acquire and transport water and chow. From these data, it cannot be determined which occurred first (food, water or object

portage), but about six months passed between Loki receiving the Frisbee and the first indications of water in the bowl.

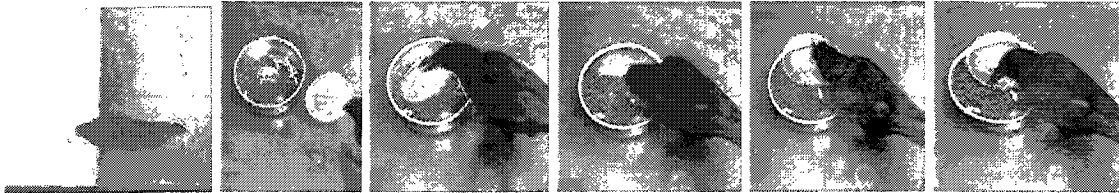


Figure 3.5 A sequence of still-frames taken from time-lapse video, showing Loki using a small Frisbee to acquire and then deliver water into his food bowl (See also DV2, Appendix D).

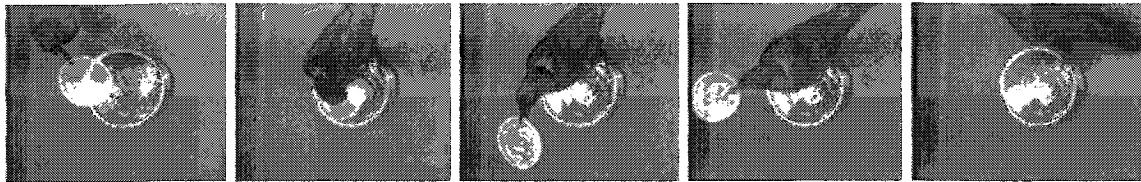


Figure 3.6 A sequence of still-frames taken from time-lapse video, showing Loki using a small Frisbee to scoop up and carry away food (see also DV3, Appendix D).



Figure 3.7 A sequence of still-frames taken from time-lapse video, showing Loki using a small Frisbee to scoop up and carry away food after the removal of a problematic object (see also DV4, Appendix D).

Observation 3: The Nozzle as a scoop and container

After Experiment 1 was over, a clear-plastic water bottle with a black plastic and stainless steel nozzle was installed on the outside of the aviary wall,

with the nozzle pointing into the aviary through the wall. It was hoped that Loki would learn to drink from it. Instead, he pushed and pulled at the nozzle until he learned to quickly dislodge the entire bottle from its holder, which would cause it to fall to the floor outside the aviary, where it was unreachable. Two weeks after the water bottle was first installed, Loki dislodged it, and it fell and shattered. The bottle was discarded but the nozzle remained on the countertop outside the aviary.

On June 19, 1999, while the Experimenter was cleaning the aviary, and the door between it and the countertop was open, Loki flew to the countertop and took the nozzle (see Figure 3.8). He was allowed to keep it for about eight months, though it had been removed from the aviary during data collection for Observation 2 (February 12 – March 1, 2000) as part of the routine rotation of enrichment objects, and was returned to the aviary May 15, 2000, where it remained for the rest of that summer and fall.

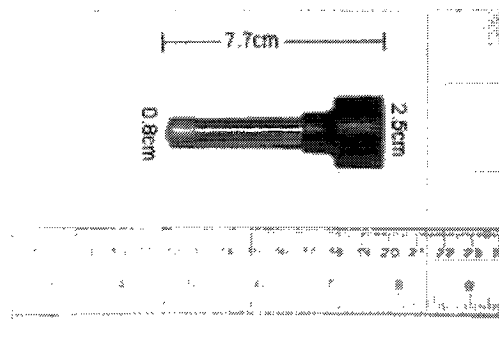


Figure 3.8 The water-bottle nozzle.

In fall of 2000, during what was intended to be bowl-baseline recording for Experiment 2 (which will be described in Chapter 4), videotape revealed Loki

placing the nozzle in the bowl, after which water could be seen dribbling from it. Occasionally he was seen actively inverting the nozzle immediately after placing it in the bowl, thus causing water to gush out. The nozzle was now also being used to take water to the bowl. Before moving ahead with Experiment 2, this new, unexpected, behavior was explored a bit further.

As stated in Chapter 2, Loki often placed non-food items in both the bath and bowl. So these apparent water deliveries could have been artefacts of post-bath nozzle deposits, which had coincidentally resulted in trapped water in the nozzle. To rule out coincidence, evidence for repeated and skillful manipulations at the bath (water acquisition) was sought.

In the beak of a crow, the nozzle can be carried in three possible orientations: cap-up (CU) or cap-down (CD), or cross-beak (CB) as seen in Figure 3.9. However, the gravity-ball in the nozzle will only fall into place and produce a watertight seal in orientation CU. In the case of coincidental water acquisitions, either no preference for nozzle orientation upon approach to the bath or upon its retrieval, or a strong preference for a single orientation upon both approach and retrieval, would be expected. However, a retrieval-preference for the CU orientation would be evidence for a skillful, learned, manipulation. An observation period was conducted to determine the relative orientations of the nozzle upon its approach to and its subsequent retrieval from the bath.

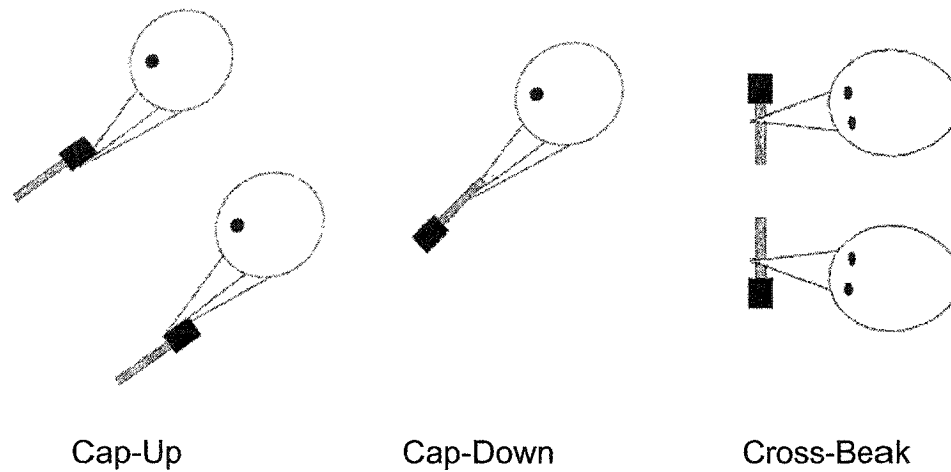


Figure 3.9 Diagrams illustrating the ways in which Loki grasped and carried the nozzle upon approach and departure from the bath. From left to right they are, as seen from the side, two cap-up (CU) views, one cap-down (CD) view, and as seen from above, two cross-beak (CB) views.

Housing, diet and novelty objects were the same as during observation 2, with the addition of a green plastic wiffle ball, a white polymer wine cork, and an orange plastic garden hose coupling (See Appendix A for a timeline, and Appendix B for photographs). The latter was the second item that Loki had taken from the countertop and was allowed to keep.

Data were collected over a two-week period (October 30 – November 12, 2000). A Sony Hi 8 camcorder (Model TR940) was mounted on the wall, at near-ceiling height, directly above the bath pan. The video and audio output from the camcorder were routed to a JVC time-lapse video recorder located in a separate room. The bath area was continually videotaped, in time-lapse mode (3 frames per second).

During the fourteen-day observation period, Loki deposited the nozzle into the bath a total of 88 times. Of those 88 instances, the orientation upon either approach and/or the retrieval could not be confidently determined in 10 instances, and the nozzle was deposited but not retrieved 3 additional times. Of the remaining 75 instances, Loki approached the bath and deposited the nozzle most often in the CB orientation (41%), second most often in the CU orientation (39%), and least often, in the CD orientation (25%). However, he retrieved it most often in the CU orientation (97%) – the only watertight orientation (see Figure 3.10).

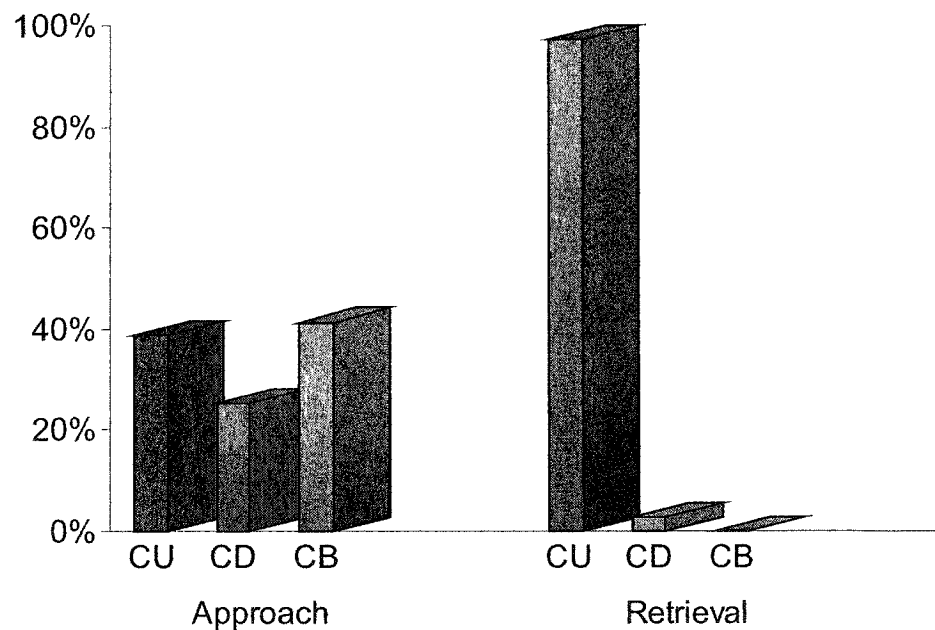


Figure 3.10. The percentage of nozzle orientations for 75 approach, deposit and retrieval incidents from the bath. CU (cap-up) is the only watertight orientation.

Upon retrieval, the water inside the nozzle could, of course, not be seen. So it cannot be positively stated that the nozzle held water on every CU-retrieval

reported here. However, near-identical human manipulations (conducted at a later date outside the aviary), using tweezers to substitute for beak suggested that it was impossible *not* to acquire water when picking up the immersed nozzle using the CU orientation. Therefore it is concluded, that the nozzle was Loki's second, and perhaps most efficient tool to date for acquiring and transporting water. From the date Loki acquired the nozzle until the first date it was seen being used to deliver water into the bowl, about sixteen months had passed – though it was absent for three months during that time span.

Observation 4: The Slinky as headscratcher

On October 16, 1999 Loki was given a multicoloured plastic Slinky (see Figure 3.11).

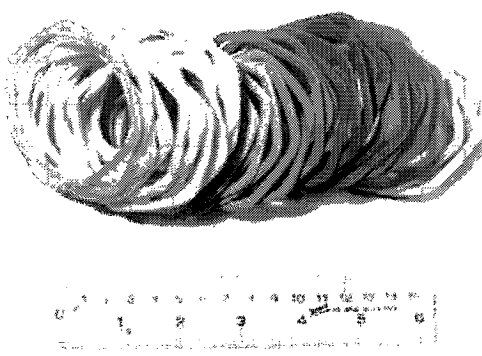


Figure 3.11 The Slinky.

Like most objects described in this chapter, the Slinky had been provided for environmental enrichment. Loki often carried toy objects to his perch, where he would hold them between his feet and peck or pull at them. The Slinky was no exception. About nine months after its receipt (July 25, 2000), the Experimenter entered the aviary for routine daily cleaning, and found the Slinky hanging from the

perch. It had been secured there by wedging some of its coils onto the perch. It continued to be found hanging from perch repeatedly over the next few years. When the Experimenter cleaned the aviary, the Slinky was removed from the perch and, as with all other enrichment objects, washed and returned to the toy corner.

During these early hangings, the Slinky was wedged across the perch at or near its middle. However, it was soon found wedged nearer to its end. Sometimes the end was wrapped two or more times around the branch. This left the free end hanging close to the floor. About a month after the first hangings were found, Loki was seen, via the remote CCTV monitor, on the floor, grasping the loose end of the Slinky in his beak, backing away with it, and releasing it. Once released, the slinky contracted, and swung like a pendulum beneath the perch. Loki was then seen to run, hop and sometimes fly at the swinging end, catching it in his beak and then repeating the exercise, continuing sometimes for up to several minutes.

Some months later (Feb 19, 2001) Loki was seen via the CCTV camera pulling at the hanging Slinky from floor-level. As it swung he moved under it and positioned his body just high enough so that the slinky repeatedly rubbed across his head and neck. When it quit swinging, he repeated the manoeuvre again and again (see Figure 3.12).

The Slinky episode shown in Figure 3.12 lasted 42 minutes from hanging to dropping it to the floor. During that time, Loki set the Slinky in motion and positioned himself underneath it a total of 37 times, in three separate bouts. This sort of behavior was seen repeatedly over the next two years, and still occasionally occurs at the time of this writing. About sixteen months passed between the time

Loki first received the Slinky and when the first headscratching episode was seen.

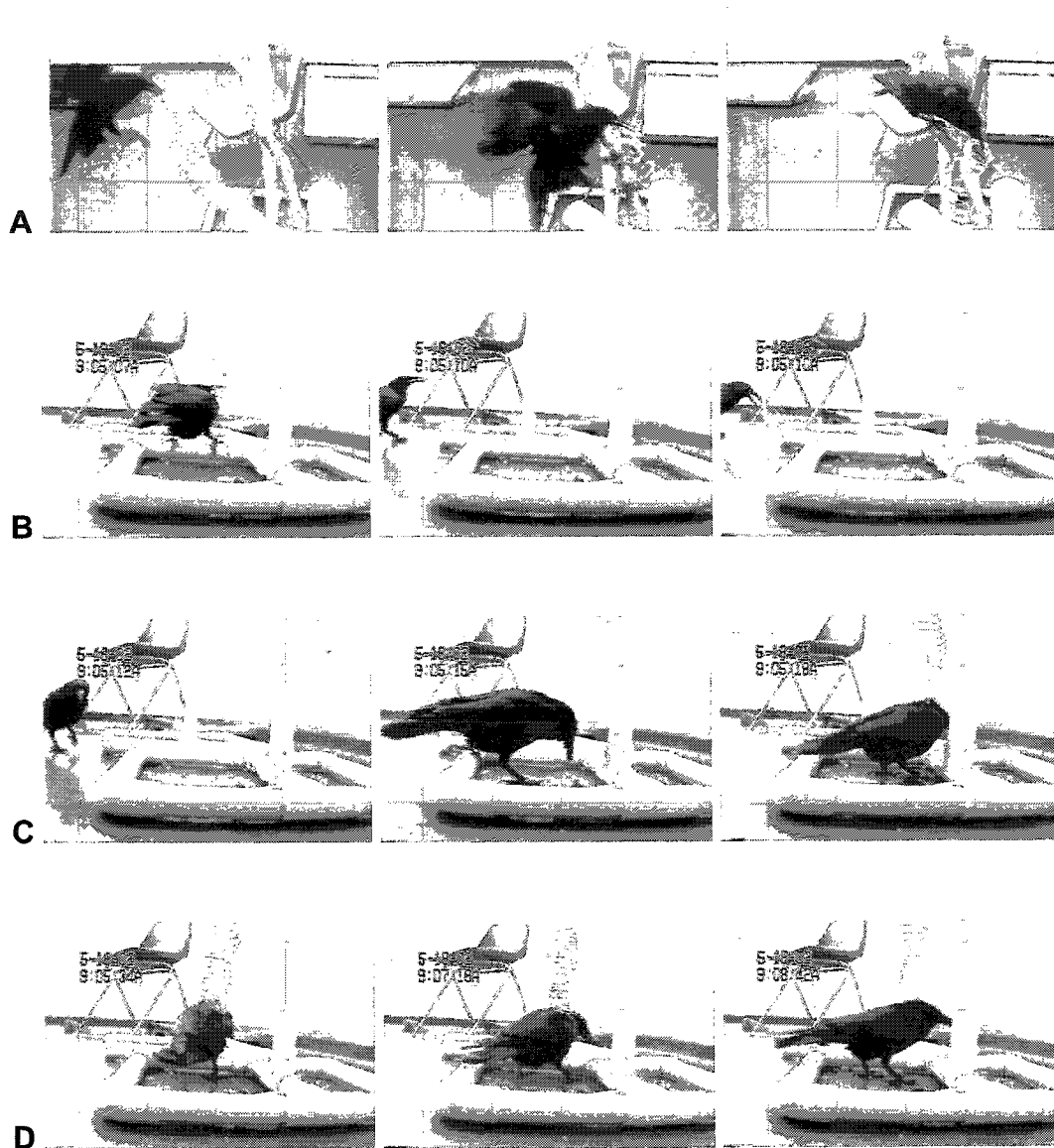


Figure 3.12 A sequence of still-frames taken from real-time and time-lapse video. Panel A shows Loki flying with the Slinky and securing it to the perch. Panel B shows Loki on the floor, grasping the Slinky, pulling it back and letting it go, thereby setting it in motion. Panel C shows Loki moving underneath the swinging Slinky until it makes contact with his head and neck. Panel D shows the end results of three subsequent pulls (see also DV5, Appendix D).

Conclusions

All of the object-directed behaviors described above fulfil Beck's (1980) definition of tool use (see Chapter 1). Loki alone was responsible for the proper orientation of unattached, environmental objects that were used to alter the form, position or condition of another object, or the user.

But *how* did these behaviors come to be? Nothing of this sort has ever been reported in free-ranging individuals, so it is improbable that these behaviors were innate. Two assertions, however, can be made. First, Loki never saw anyone engaging in similar behaviors with these objects. This, coupled with the negative results reported in Chapter 1, strongly suggest that imitative learning could not have been a contributing factor. Second, these behaviors came into being only after extended periods of object exposure – from 6 to 16 months. Any other information regarding the development of these behaviors could only be, at best, educated speculation. Data chronicling Loki's interaction with a new object, from first exposure through to its use as a tool, would be required.

Chapter 4

The Cup

Numerous instances of tool use and even tool modification by crows have been published in the scientific literature, many after only a single sighting of a single individual (see Table 1, Chapter 1). Most published tool use reports involve individuals with unknown histories, thus making it impossible to trace the origin or ontogeny of the tool use. Chapter 3 also reported several acts of tool use by a crow. This particular tool user's history was known, but only the end-results of his tool use were seen, so developmental details remained unknown. The objective of the present study was to document the development of Loki's interactions with a novel object from first exposure through its use as a tool. To do so, an unfamiliar object was introduced into the aviary, one which *if utilized* would be a more efficient water portage tool than either the Frisbee or the nozzle and, because none of the water acquisition manoeuvres that worked with the prior tools would be appropriate for this new object, would also require the development of a new skill-set.

Understandably, this was a gamble. There were several possible outcomes. Loki might never interact with the object, though this was unlikely given his penchant for manipulating things. He might interact with it, but never use it in a tool-like way, as was true of most of the enrichment objects available to him. Or, perhaps by insight, he might immediately upon receipt begin using the object for water acquisition and portage. This also seemed unlikely given the extended developmental periods reported in Chapter 3. It seemed most

probable that Loki would have to spend time manipulating and learning the characteristics of this new object. How much time was anyone's guess, but it was hoped that along the way his behavior would reveal something about the ontogeny of tool use behavior.

Method

Housing and Diet

Housing and diet were the same as during Observation 4, with the following exceptions: a new tree-branch holder (perch) made of white ABS tubing had been installed, and the small bowl was no longer in use (see Figure 4.1 for the aviary layout, and Appendix A for the timeline).

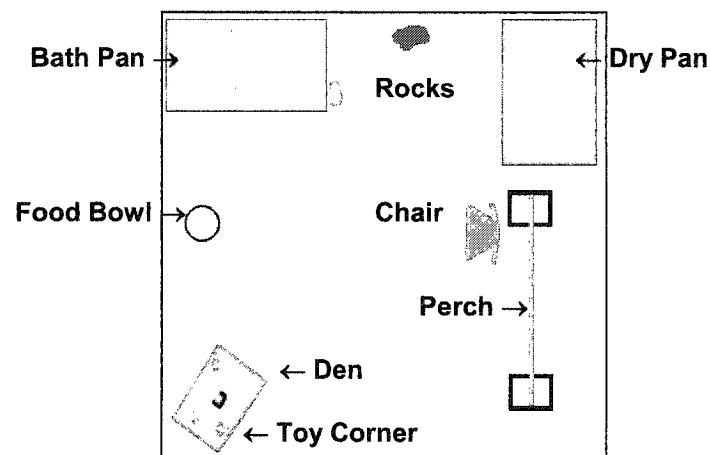


Figure 4.1 A schematic of the aviary layout during Experiment 2 (not to scale).

Apparatus

Familiar objects present in the aviary during this experiment were the Frisbee, nozzle, spool, hose coupling, wiffle ball, white ball, polymer cork, key

chain, slinky, link chain, PVC ring, and a funnel tip (see Appendix A for their introductory dates and Appendix B for photographs). For this experiment, two new objects were introduced, a small, green, plastic cup capable of holding 107ml of liquid, and an identical cup from which the bottom had been removed (see Figure 4.2). The bottomless cup was essentially a ring and will be referred to as such. Both of these objects were identical 2.95 litre detergent bottle caps (Tide brand) that, after the rims were removed, measured 5cm in diameter and 5.5cm in height.

Procedure

On December 4, 2001, as part of the daily aviary cleaning, the cup and ring were left among the pile of familiar toys in the toy corner.

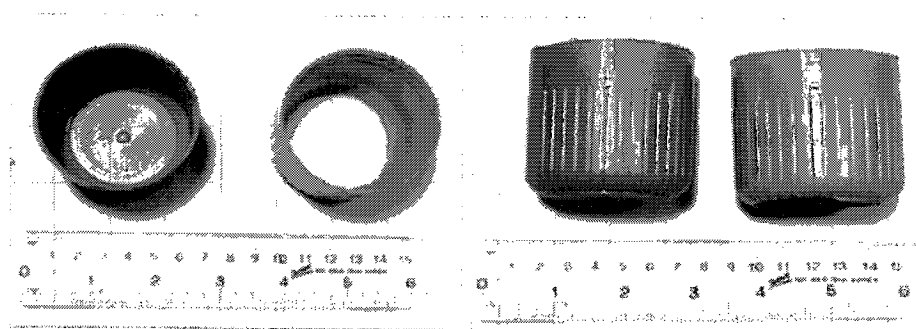


Figure 4.2 The two modified detergent bottle caps used in Experiment 3.

Data Collection

Tracking

Each day, prior to cleaning, the Experimenter looked for any telltale evidence that water was being acquired or transported, such as the presence of water in the cup or food bowl, or puddles around the aviary.

Real-Time Observation

The CCTV camera and microphone (described in Chapter 3, Observation 2) remained in place and continued to provide an overhead view of the entire aviary. This view was fed to two monitors in two separate, nearby rooms. This provided a venue for remote real-time observation. At least one trained observer was near a monitor each day during the aviary's light phase (8:00am – 8:00pm). Most of Loki's activities produced very distinct sounds, and these sounds alerted the observer to pay attention and make notes regarding activities at the bath or bowl.

Time-Lapse Video Recording

Additionally a Sony Hi 8 camcorder (Model TR940) was mounted on the wall, at near-ceiling height, above the bath. A second Sony Hi 8 (Model TR3400) camcorder was similarly mounted above the bowl. The video and audio outputs from the bath-camcorder were routed to a JVC time-lapse video recorder (model SR-L900U) located in a separate room, and the video and audio outputs from the bowl-camcorder were routed to a Panasonic time-lapse video recorder (AG6730).

Video data were collected for 168 days in total and data were divided into 14 Blocks of 12 days each. During Blocks 1 – 3, the bath and bowl area were continually videotaped, in time-lapse mode (3 frames per second). However, in Block 4, the JVC recorder was unavoidably taken out of service. At that time the video and audio outputs from both camcorders were routed to a switcher, which provided manual control over which set of outputs was sent to the remaining Panasonic time-lapse video recorder (AG6730). For Blocks 5 – 14, the input to the recorder was alternated daily, immediately after the aviary was cleaned, on a revolving schedule so that the bath area was recorded one day and the bowl area was recorded the next (in time-lapse mode, 3 frames per second).

Videotapes were reviewed daily for behavior involving either the cup or the ring, and descriptions of the many different types of object interactions seen at the bath and bowl were recorded in a written commentary. These descriptions were categorized and tabulated to provide frequency counts, organized into 12-day Blocks, each representing 6 days (about 72 hours) of bath and bowl interactions, to answer the following questions:

- (a) What were the relative deposit rates of both cup and ring at the bath?
- (b) How often were cup deposits in the bath followed by subsequent retrievals, and was the cup holding water upon its retrieval?
- (c) How often did the cup contain a food or toy object upon its deposit into the bath?
- (d) What were the relative deposit rates of both cup and ring at the bowl?

- (e) How often did the cup contain water upon its deposit into the bowl, and how often was that water actively expelled into the bowl?

Results

Cup and Ring Activity at the Bath

Loki put the ring into the bath for the first time 2 ½ hours post-availability. The cup was not deposited there until 27 ½ hours had passed. Nonetheless, during the first Block of data collection, the cup was placed in the bath almost twice as often as the ring. Then bath-related manipulations for both items waned quickly (see Figure 4.3).

Water Acquisition

Loki persisted in using the Frisbee and nozzle for moving water and food, and his relative interest in the new objects was minimal after 8 weeks of availability. So early in Block 6 the Frisbee and nozzle were removed from the aviary. Finally, approximately 3 months later, during Block 13, cup activity at the bath increased dramatically. There was no similar increase in ring deposits (Figure 4.3).

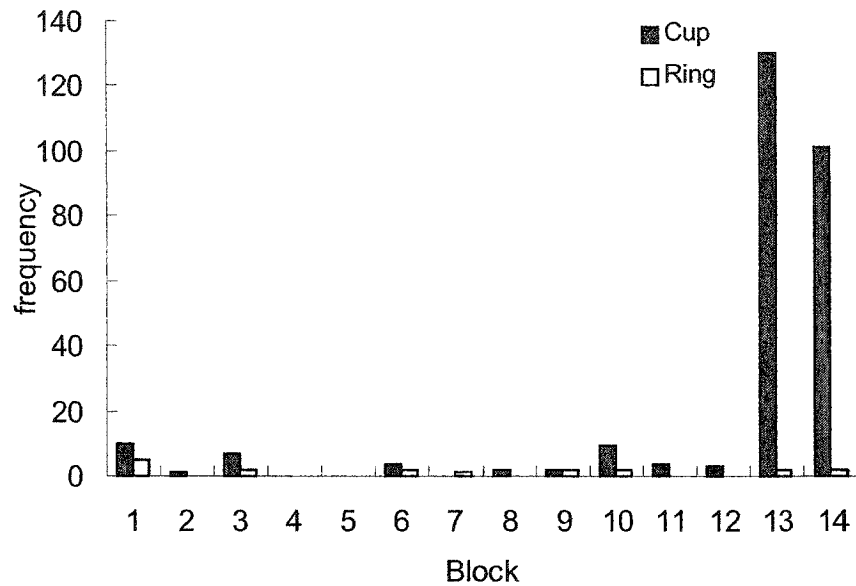


Figure 4.3 Relative frequencies of cup and ring deposits into the bath for 14 Blocks (12 days each).

During Block 13, at 144 days post-introduction, water could be seen in the cup as it was carried away from the bath (May 1, 2001). See Figure 4.4 for a relative comparison, across Blocks, of frequencies of cup deposits in the bath, subsequent retrievals of the cup, and the number of those retrievals in which water could be seen in the cup (water acquisition). Convergence of the three bars within a Block would indicate that all cup deposits at the bath resulted in water acquisition, and for Block 14 this is nearly so; 101 deposits resulted in 97 water hauls. Loki had finally learned to use the cup as a water acquisition tool.

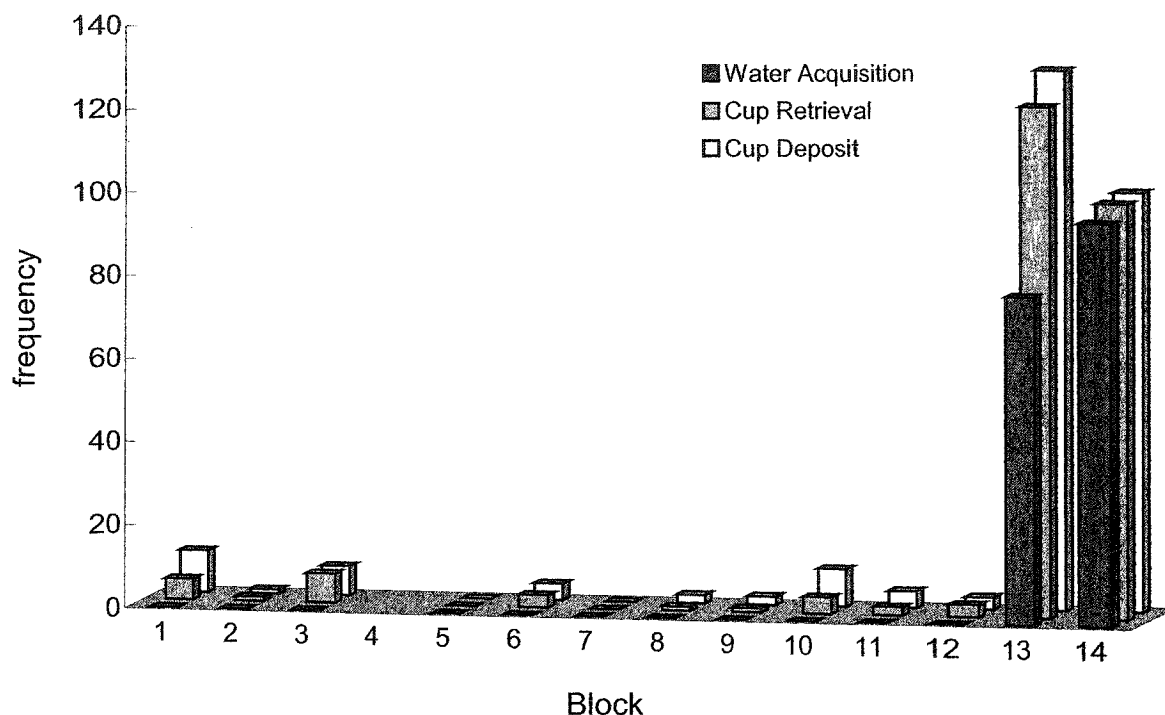


Figure 4.4 The frequency of cup deposits and subsequent retrievals at the bath, and the number of those that resulted in water acquisition, for 14 blocks (12 days each).

Cup and Ring Activity at the Bowl

The cup, rather than the ring, was the first of the two items to go into the bowl, at 25 ½ and 50 ½ hours respectively post-availability, though of course it held no water at that time. Just as had occurred at the bath, activity at the bowl involving the objects waned and became nearly nonexistent until Block 13 (see Figure 4.5), when the cup began to be deposited into the bowl again after a six Block hiatus. There was no similar increase in ring deposits.

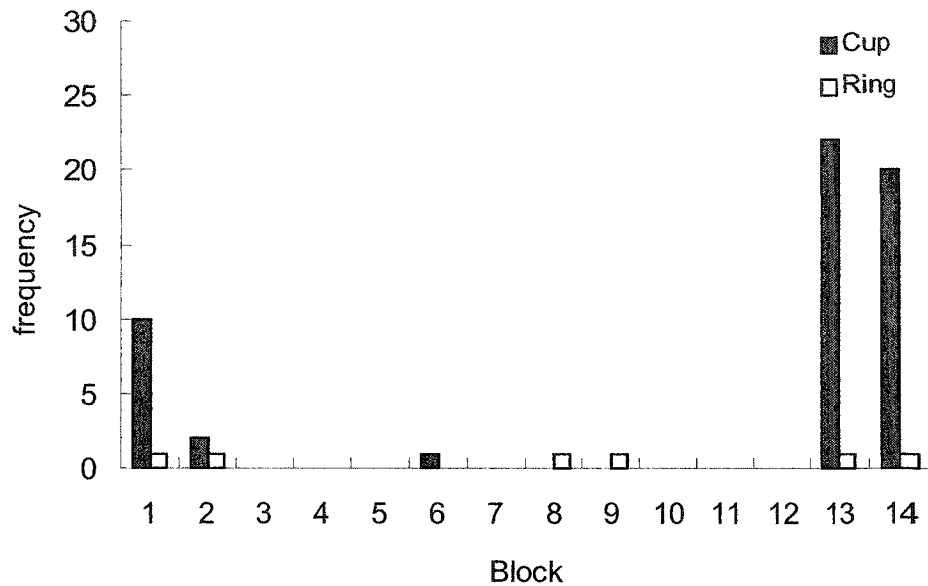


Figure 4.5 The frequency of cup and ring deposits into the bowl over 14 blocks of data collection (12 days each).

Water Portage

At 146 days post-introduction (April 29, 2001), Loki placed the partially filled cup in the bowl, but instead of pouring the water into the bowl, he retrieved the cup almost immediately and carried it off camera, in the direction of the bath. The next day puddles were found on the dry pan with the cup lying nearby, and two days later the food in the bowl was awash with water (May 2, 2001).

A comparison between the total number of cup deposits into the bowl, the subset of those for which the cup held water, and then finally the further subset for which the water was actively poured into the bowl, can be seen in Figure 4.6. The convergence of all three bars within a Block would indicate that each time the cup went into the bowl the water was poured out, but this did not occur. In Block 13, the cup contained water on 59% of its deposits, and only 31% of those

were poured into the bowl (4 out of 13). But in Block 14 these figures increased to 65% and 92% (12 out of 13) respectively.

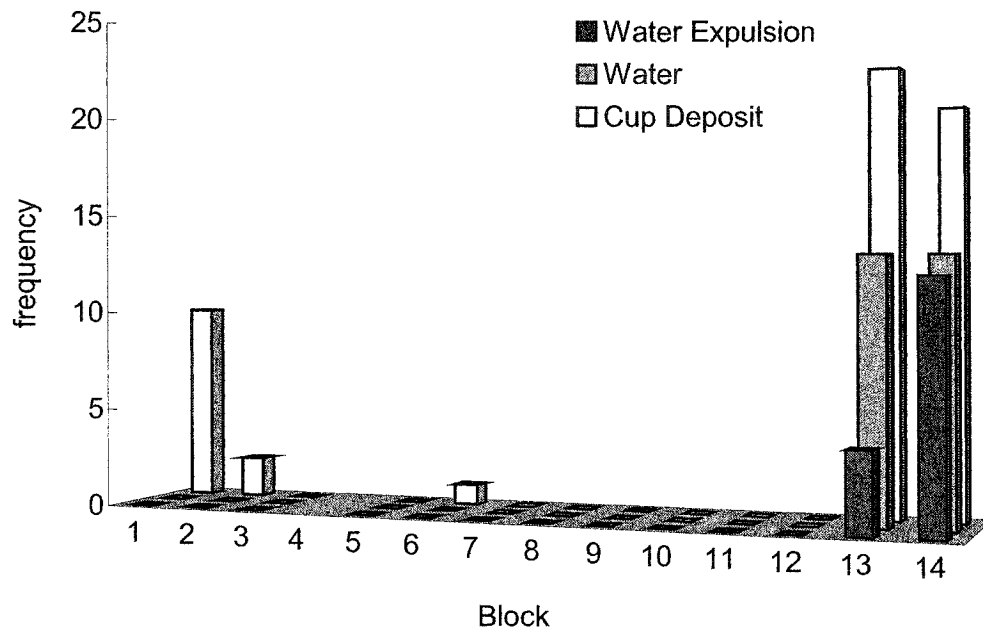


Figure 4.6 The frequency of cup deposits, with water, and water expulsions made into the food bowl, for 14 blocks (12 days each).

At first glance, the sudden increase in cup-related behavior at the bowl in Blocks 13 and 14 (Figure 4.6) might rouse thoughts of insight learning. But reducing the last two Blocks into smaller segments of 3 days each (see Figure 4.7) shows no water expulsions during the early days of Block 13 (segments 13-1 and 13-2), increasing to a 33% rate (13-3 and 13-4), a 67% (14-1), and finally a 100% rate, for the final three segments (14-2, 14-3, 14-4). This pattern reveals a slow rate of learning occurring over the course of 24 days, which is inconsistent with insightful learning.

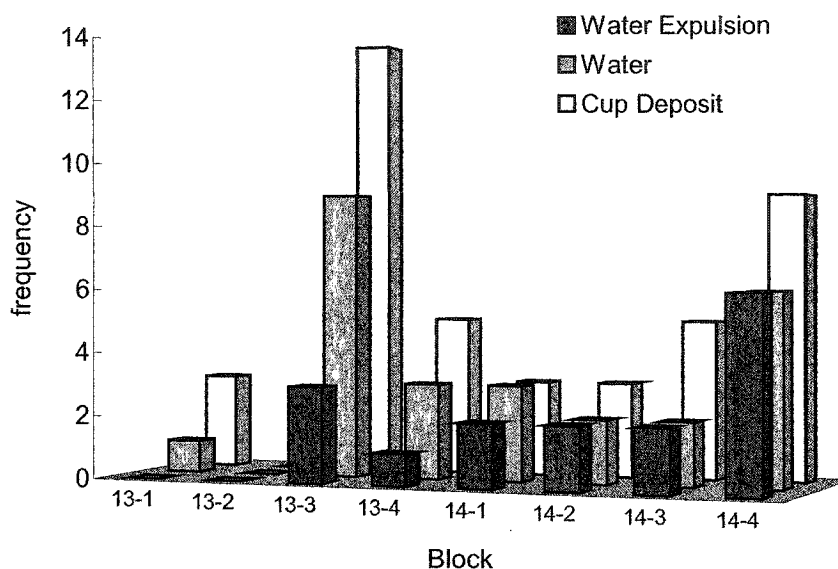


Figure 4.7 The frequency of cup deposits, with water, and water expulsions made into the food bowl, in groups of 3 days each for the last two blocks of data collection.

It should be remembered that if simply dropped into the water (like the nozzle), the cup would only float, and even if forcefully pressed down in the middle (like the Frisbee), it was too tall to submerge, so the question still remained as to how Loki initially managed to get water *into* the cup.

Food and Object Portage

Water was not the only thing that Loki carried in the cup. It was also used for food and toy portage, but only for smaller toys and larger pieces of food, which were picked up in the beak and placed in the cup. The combinations were then carried either to the bath or out of camera view. Long-term, casual observation of Loki's daily activities showed that he spent a large portion of his day in activity, and much of that activity consisted of the combining and

recombining of mobile objects, along with the caching of objects and food anywhere they would fit. Novel items always received a larger share of interaction for several days post-introduction. So it was not surprising to see items being transported in the cup even very early in the study (see Table 3).

Table 3 shows the frequency of cup deposits into the bath for all 14 Blocks, along with the number of those deposits in which the cup carried a toy or a food item (combination deposits). Data are missing for Block 4.

As can be seen, a total of 18 deposits were made during the first three Blocks, 5 of which were combination deposits. After that, combination deposits were not seen again until Block 10. These increased dramatically, along with empty-cup deposits, in Blocks 13 and 14.

Block	Empty Cup	Cup + Food	Cup + Toy	Block Total
1	7	1	2	10
2	0	1	0	1
3	6	0	1	7
4	—	—	—	—
5	0	0	0	0
6	4	0	0	4
7	0	0	0	0
8	2	0	0	2
9	2	0	0	2
10	8	1	0	9
11	3	1	0	4
12	1	2	0	3
13	58	21	51	130
14	33	11	57	101

But, more importantly, food and toy portage may have played a role in the development of Loki's water acquisition skills by making the cup easier to manipulate at the water source. Figure 4.8 shows the proportion of cup deposits into the bath for which the cup contained nothing, food, or a toy for the last 7 Blocks of data. This figure indicates that empty cup deposits decreased, food portage increased and then decreased, while toy portage increased.

It seems counterintuitive that Loki would reduce food portage in favor of carrying inedible objects to the bath. However, a close look at the videotapes revealed that when the cup contained an object, it often tipped to one side as it

was placed in the water and a then a few pushes with the beak sufficed to fill it (see Figures 4.9 and 4.10). Occasionally an object upset the balance enough that the cup fell over onto its side and filled as soon as it was deposited (see Figure 4.11).

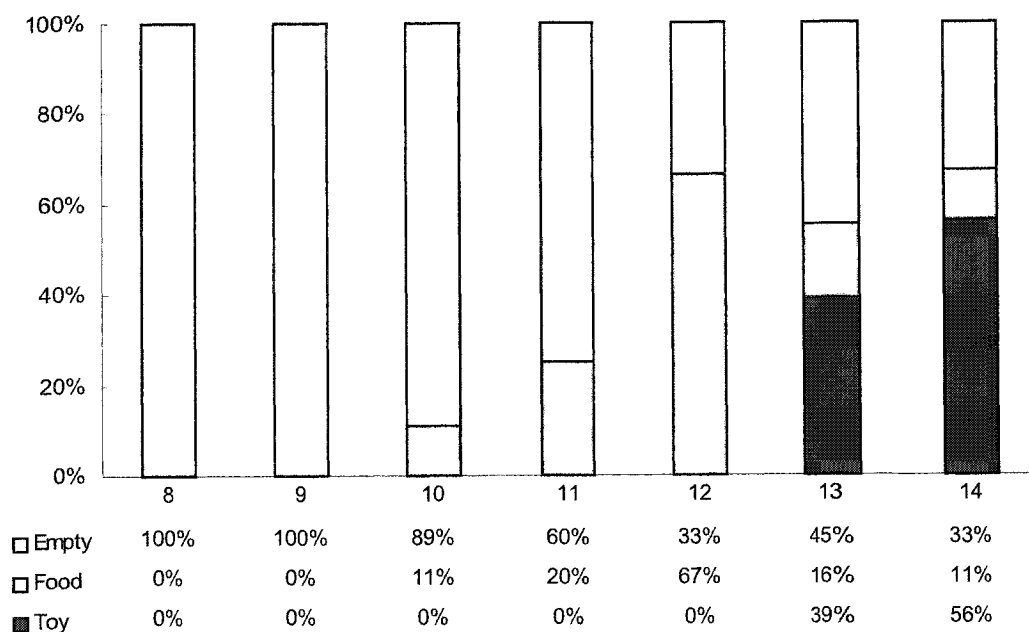


Figure 4.8 The percentage of cup deposits into the bath in which the cup carried nothing, a toy or food for Blocks 7 - 14 (12 days each).

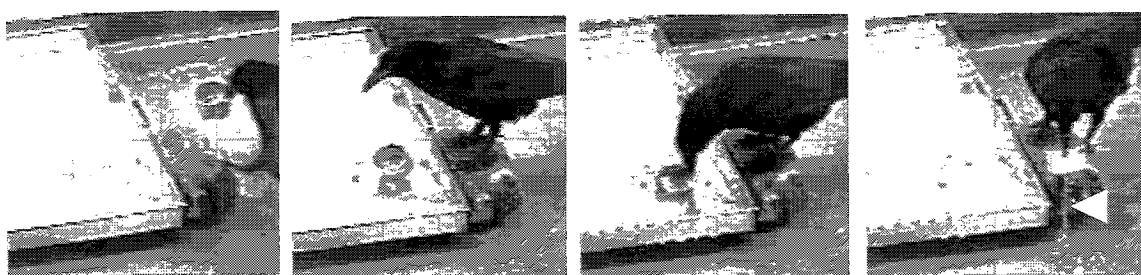


Figure 4.9 A sequence of still-frames taken from a May 6, 2001 time-lapse video showing Loki approaching the bath with the cup in his beak; the keychain is inside. Once deposited, the cup is tipped over somewhat by the weight of the item inside. With a beak-push the cup's edge submerges and fills, and water (arrow) can be seen spilling from it as it is carried away (see also DV6, Appendix D).

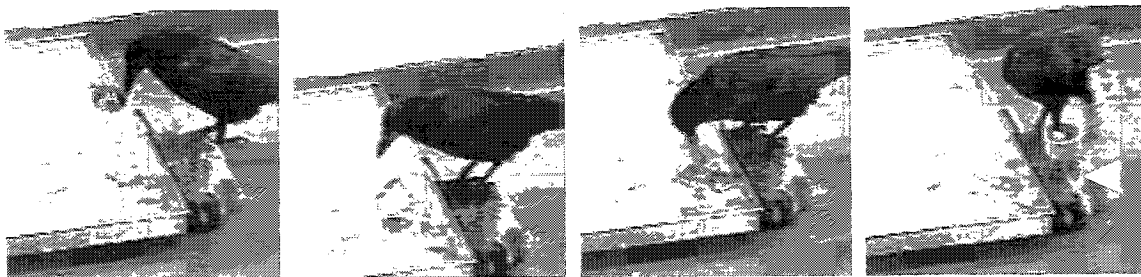


Figure 4.10 A sequence of still-frames taken from a May 6, 2001 time-lapse video showing Loki approaching the bath with the cup in his beak, the orange plastic hose coupling is inside. Once deposited, the cup is tipped over somewhat by the weight of the item inside. With a beak-push the cup's edge submerges and fills, and water (arrow) can be seen spilling from it as it is carried away (see also DV7, Appendix D).

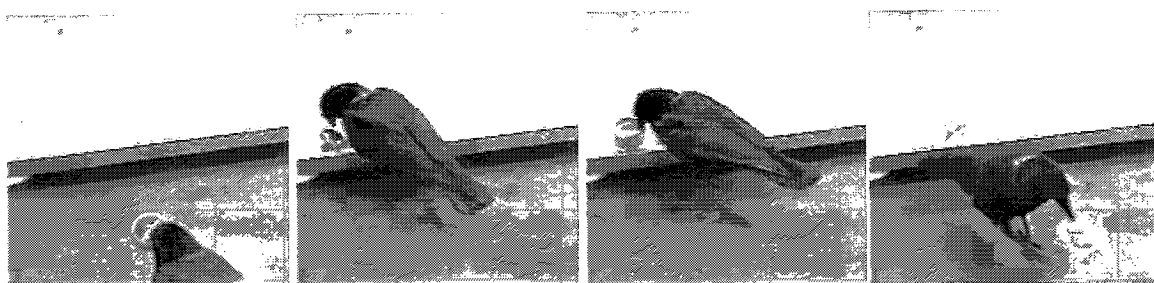


Figure 4.11 A sequence of still-frames taken from a May 6, 2001 time-lapse video showing Loki approaching the bath with the cup in his beak. Note the green toy object inside the cup. Once deposited, the cup fell onto its side as a result of the relatively heavy item it contained. In this particular instance, when Loki retrieved the water-filled cup and carried it away, the toy remained in the bath (see also DV8, Appendix D).

The objects made the cup less stable and less buoyant, which appeared to make it easier to manipulate, which should have resulted in a higher rate of water acquisition for cup and toy deposits when compared to empty cup or cup and food deposits. Figure 4.12 shows a comparison of water acquisitions during Blocks 13 and 14 as a function of whether the cup was empty or contained food

or a toy. While all types of deposits resulted in water acquisition to some extent, in Block 14 cup and toy deposits resulted in a 95% water acquisition rate.

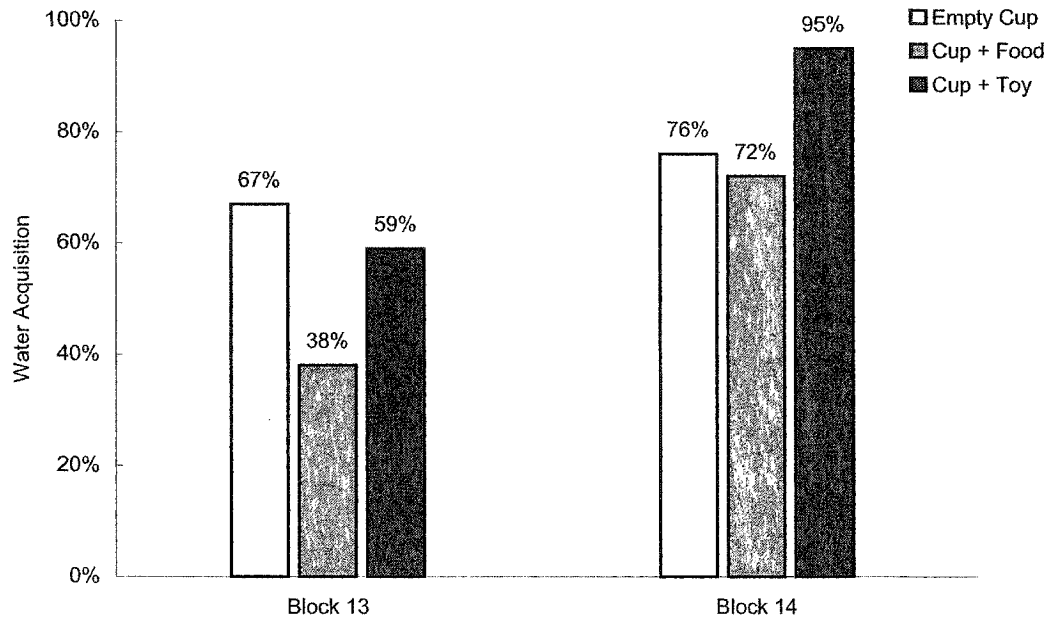


Figure 4.12 shows the percentage of cup retrievals at the bath in which water was acquired as a function of whether the cup was empty upon its deposit, or contained a food or toy item, for Blocks 13 and 14.

Loki's cup manipulations at the water source were quite different from those used with either the Frisbee or the nozzle. He developed three different strategies to fill the cup. He was seen depositing the cup while grasping its nearest edge in his beak and then twisting his head laterally from side to side as he placed the cup in the water – which resulted in a sweeping sideways motion. He was also seen placing the cup flat on the water's surface and then grasping the cup by one side repeatedly pressing it over onto its side and down into the water. Finally he was seen carrying food and toys to the bath in the cup, which if the item possessed sufficient weight and size caused the cup to tip over

completely and fill, or to sit lopsided in the water. Then Loki would push the broad side of the cup, which caused the edge nearest the water to submerge (see Figures 4.9, 4.10, 4.11). All of these manipulations sufficed to get water into the cup.

Conversely, the expulsion manipulation seen at the bowl was somewhat similar to that used with the Frisbee. The cup was placed inside the bowl and then pushed over by pressing the top of the upper mandible against the cup's upper edge, or the nearest edge of the cup was grasped in the beak and the cup was laid over by tucking the head downwards (see Figure 4.13).

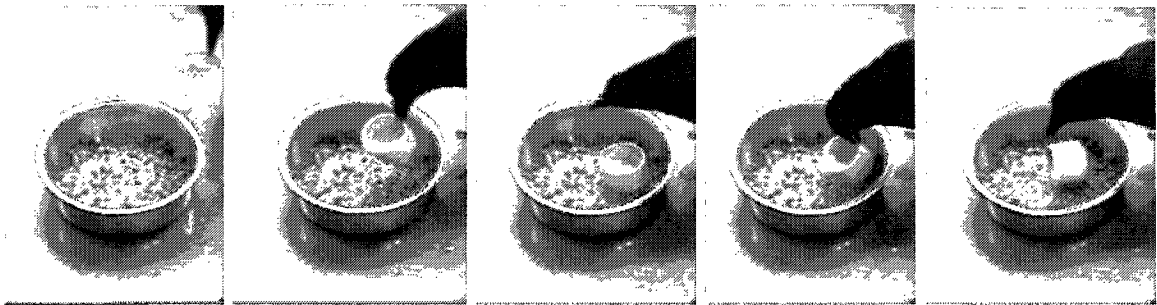


Figure 4.13 A sequence of still-frames taken from time-lapse video, showing Loki placing a water-filled cup into his food bowl and then pouring out the contents (see also DV9, Appendix D).

Post-Experimental Data

After Block 14, the view from one camera was expanded to encompass both bowl and bath, and additional data were collected for another 14 days (Day 12 data are missing because of an equipment failure). From this height, there was not enough resolution to see the finer details of Loki's cup manipulations at either

site, but one could see if water was acquired at the bath and subsequently poured into the bowl.

Figure 4.15 shows that water acquisition continued to be a daily occurrence throughout the 14-day post-experiment observation period. However, Figure 4.16 shows that water deliveries to the bowl did not occur every day (11/14 days), and a combined comparison shows that more cups of water were acquired every day than were actually poured into the bowl (Figure 4.17).

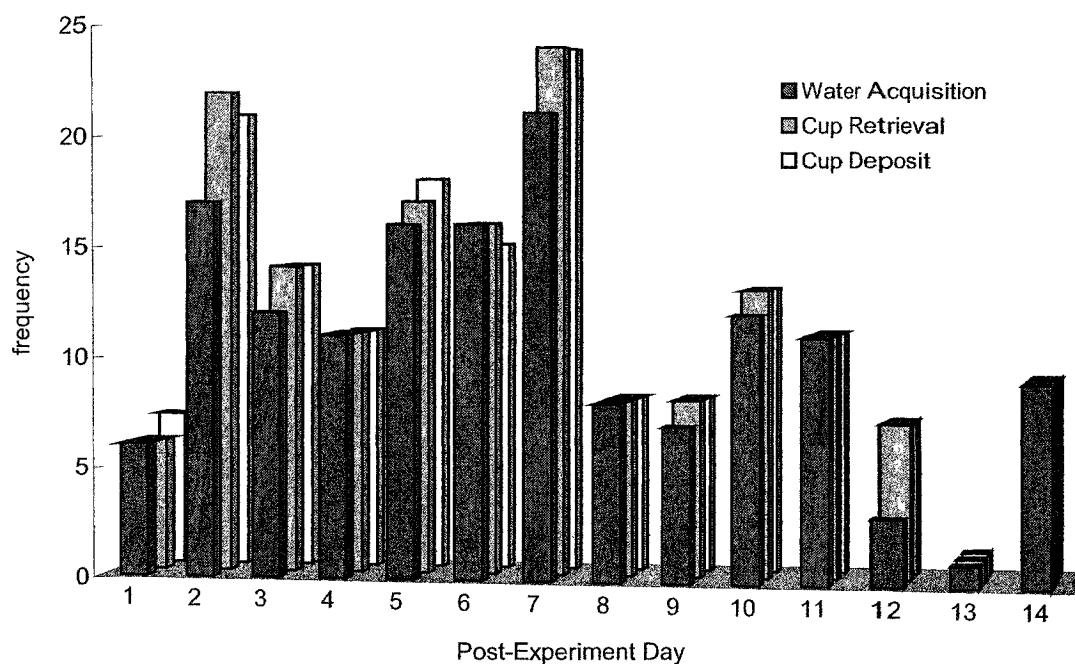


Figure 4.15 The number of cup deposits, retrievals, and water acquisitions at the bath, for fourteen additional days post-experiment. The cup retrieval data for Day 2 and Day 6 show more retrievals than deposits. In both cases, the discrepancy represents the retrieval of a deposit made on the prior evening.

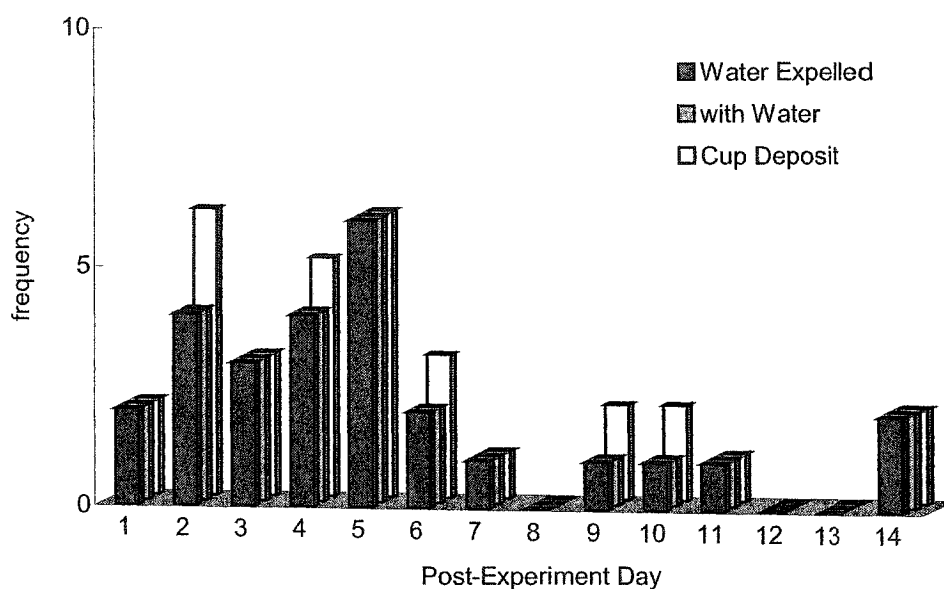


Figure 4.16 The number of cup deposits, with water, and water expulsions made into the food bowl, for fourteen additional days post-experiment.

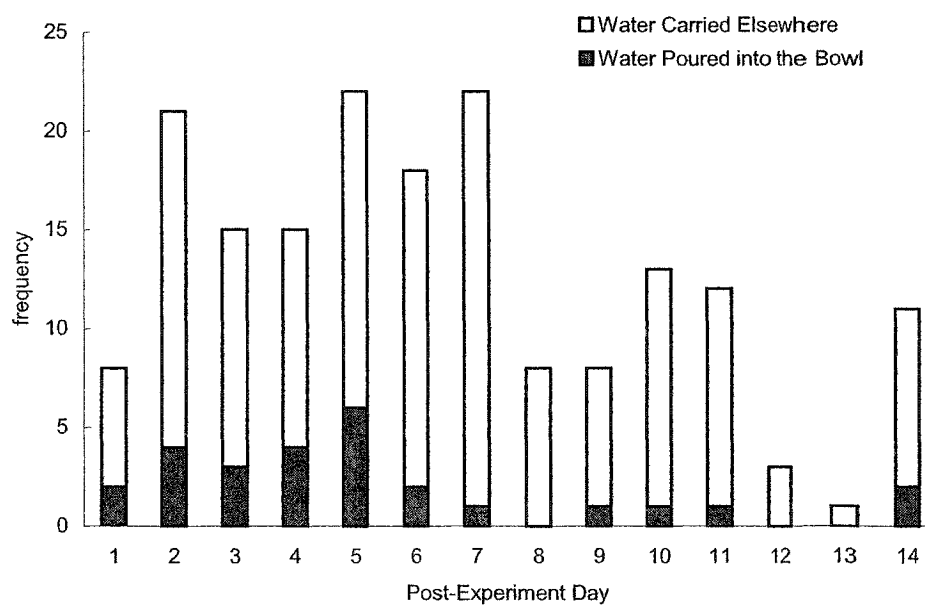


Figure 4.17 Each bar represents the total number of cups of water that were acquired that day. The dark portion of the bar shows the number of those cups that were poured into the bowl; the remainder were carried off-camera.

Conclusions

Clearly Loki learned to use the cup to acquire and transport water from the bath, and also to deliver and expel that water into his food bowl - and he required 5 months to do so (Dec 4, 2000 – May 2, 2001). It is possible that he might have learned to use the cup sooner, had the two preferred tools (Frisbee and nozzle), been removed before the cup was introduced. But, even then, it is doubtful that he would have done so in less than the 3 additional post-removal months. Loki's behavioural development showed a steady, progressive, development of tool use behavior resulting, first, in the act of water acquisition and, finally, water expulsion into the bowl. The lengthy developmental period, as well as incremental behavioural changes, are inconsistent in terms of (based on) insight, and support instead the development of tool use from the modification of species-typical behaviors (caching and food-soaking) through Thorndikian and operant conditioning. The question of why the cup might have been taken to the bath in the first place will be addressed in the General Discussion (Chapter 6).

The cup was also used for food portage and toy portage, but only for smaller toys and larger pieces of food, which were picked up in the beak and placed in the cup, and then the combination was carried away. Loki did not develop a strategy, in the time allotted, to use the cup as an acquisition tool for the smaller bits of food (as he had with the Frisbee). He may simply not have had enough time, or there may have been no need to do so; for the cup delivered enough water to the bowl that the chow was soaked after only one or two water delivery trips.

Consistent water acquisition occurred only after food and object portage, suggesting that these behaviors may have influenced the development of Loki's water acquisition skills by initiating the tipping motion necessary to submerge the cup's edge under the water's surface. Even after Loki had developed the behavioural strategy to acquire water with the empty cup, he still displayed a preference for making cup and toy deposits ($f = 57$), rather than cup and food ($f = 33$) or empty cup deposits ($f = 11$) in Block 14. This preference may have emerged because including toys in the cup resulted in a higher rate of water acquisition (95% rather than 76% or 72% in the last data block). The use of a second object to enhance the suitability of a tool for a specific job, either by increasing its efficiency or its ease of use, could be considered tool modification¹⁷ that, in this case, was operantly conditioned.

However, not all acts of water portage concluded at the bowl. In fact, only a fraction of them did. Where was the additional water going, and what was Loki doing with it once it got there? It is unfortunate that the entire aviary was not simultaneously recorded for the duration of the 6-month study. However, Loki's behavior left tracks that were indicative of his activities, and that were noted by the Experimenter prior to cleaning the aviary each day. These tracks suggested that Loki had extended his tool use repertoire in yet another way.

During daily inspection puddles were seen around the aviary floor, and in the dry pan along with food remnants. Loki traditionally used the flat rock near

¹⁷ Tool manufacture has been defined as "any modification of an object by the user or a conspecific so that the object serves more effectively as a tool" (Beck, 1980). Loki's behavior seems to fulfill this definition, but is more appropriately characterized as tool modification.

the bath as an anvil. He would dip larger food items (usually dog biscuits, though fruits and vegetables too) into the water, then hold them under one foot (known as *tether-footing*) or between both feet as he stood on the rock, and peck or pull them apart. However, based on the puddles and smeared food remnants, it appeared that some of Loki's culinary preparations had begun taking place inside the dry pan - and that he occasionally moved both water and food there to do so. No food-related purposes could be determined for the remaining puddles found on the aviary floor.

Chapter 5

Memory, Efficiency and Play

As reported in Chapters 2 and 3, from a very early age Loki carried food in his beak to the water pan and moistened the food before eating it. He later used tools to transport both food and water in ways that seemed more efficient than using only his beak (Chapter 3), and finally he learned to use a small cup to acquire and transport water. Cup use permitted the moistening of entire bowls of food with only one or two water deliveries (Chapter 4). Presumably moistening the food makes it more palatable, digestible, or perhaps easier to exploit (e.g., the shells of nuts may become weaker and easier to break after prolonged soaking).

However, post-experimental data in Chapter 4 suggested that Loki's water portage might also be serving purposes that were not food-related. Observations made in the months that followed the cup experiment revealed Loki using the cup to make puddles in various places around the aviary. After pouring the water out, he would sometimes place his head parallel to the floor where he then appeared to be either drinking the water or smearing it about by using sweeping motions with his beak. He also often grasped the empty cup in his beak and swished the bottom of it around in the puddle, or rubbed other toy objects around in the puddles (Frisbee, link chain, keychain, hose coupling, etc.). These behaviors, as well as many others, seemed to have no apparent purpose other than play. This called into question whether water deposits to the bowl were actually acts of "efficiency" or whether they too fell under the category of "play".

One way to test this possibility would be to give Loki pre-moistened chow so that water deliveries would become unnecessary. Unfortunately, two concerns caused this approach to be abandoned. First, each day when the caretaker provided Loki with a fresh bowl of food, it included not only chow but also larger food items such as dog biscuits, tuna, cheese, dry pasta, carrots, etc. Typically, Loki consumed these larger food items first, or removed them from the bowl, before he poured water into it. Providing a bowl of pre-moistened chow, which on any given day might also include cheese, tuna, or other perishable items, invited, over a 24-hour period, a bacterial soup. Serving a bowl of pre-moistened chow without the larger food items was a possible alternative. However, Loki can be quite neophobic, and is especially suspicious of changes in his food. He has been known to boycott the food bowl for more than 24 hours when new food items have been placed in it without their first having been introduced to him via the caretaker's hand (i.e., social facilitation). So serving food that might quickly spoil, or serving even familiar food items in a different way, could have produced changes in Loki's food-related behavior that had nothing to do with the moisture level of the chow. These disadvantages raised too many concerns regarding health risks as well as experimental confounds to warrant the use of this experimental approach. An alternate experiment was conceived that did not change the appearance of the food, but which might encourage one kind of behavior over another. The bowl, in its original location, was fairly close to the bath. An increase in the distance between food and water would increase the energy required to make water deliveries to the bowl. If water

deliveries to the bowl were acts of efficiency, increasing the energy required to do so should have little or no effect on water deliveries. One or two water deliveries would moisten all the food in the bowl, and this would still seem to be more efficient than making many food delivery trips to the bath using the Frisbee. However, if water deliveries to the bowl were acts of play, increasing the distance might make the act one of diminishing returns. In this case, water deliveries to the bowl might stop altogether or deposits might be directed elsewhere – perhaps closer to the water source, or in the location where the bowl used to reside. Moving the food bowl around within the aviary seemed like a less intrusive manipulation than changing the way the food itself was served, i.e., one which would be less likely to provoke a neophobic reaction/experimental confound.

The set of experiments reported in this chapter investigated the effects increasing the distance between the bowl and the water source had on Loki's water and food portage behavior.

In addition, this experiment also offered the unique opportunity to test Loki's memory for a learned tool use act. At the time of these experiments, the Frisbee and the cup/ring had not been in the aviary for 27 and 15 months respectively. The efficient use of tools after such a lengthy absence might require a relearning period. Several studies have been published on some Corvid species' astounding memory for cache sites (Balda & Kamil, 1989, 1992; Bednekoff, Balda, Kamil, & Hile, 1997; Clayton & Dickinson, 1999a, 1999b; Kamil

& Balda, 1985), but nothing is known about retention intervals for a learned tool-use act in this group of birds.

Method

Housing and Diet

Loki was moved to a different room (1277) in the Dalhousie University Psychology Department's animal housing facilities on March 22, 2003. This room was nearly the same size as the old one, and all items from the previous aviary were arranged in the same relative layout in the new aviary. Diet was the same as during Experiment 2.

Apparatus

The toy objects present in the aviary during this experiment were the same as in Experiment 2 (pictured in Appendix B). Three objects, two of which had been used as portage tools in the past but which had not been in the aviary for extended periods of time, were reintroduced: the Frisbee (absent for approximately 27 months) and the cup and ring (absent for approximately 15 months). The Frisbee, cup and ring were available for all conditions except for C and D, when the Frisbee was removed.

The CCTV camera and microphone (described in Chapter 3, Observation 2) remained in place and continued to provide an overhead view of the entire aviary. A second video camera (Sony Hi 8 model TR940) was mounted on the wall, at near-ceiling height above the food bowl, which was located in one of two possible locations depending upon which condition was in effect. For Condition

A, the camera was zoomed in to focus on the bowl and bath area, and for all other conditions it was focused only on the bowl.

Procedure

Seven conditions were conducted for this experiment. Details, including bowl placement, camera set-ups, and the questions each condition attempted to answer, can be seen in Table 4.

Two weeks of Baseline data, consisting of a record of the activities occurring at both the bath and bowl involving either food or objects, were collected prior to the reintroduction of the objects. This was done to ensure that additional forms of tool use had not developed during the break between this and the last experiment.

Then, on May 12, 2003, as a part of the daily aviary cleaning, the Frisbee, cup and ring were left among the pile of familiar toys. Seven experimental conditions were conducted over the next 19 weeks. During that time, the food bowl, which was normally located 83.5cm away from the nearest point to the water source, was systematically moved back and forth between the original location (O) and its farthest possible point (F) from the water source (221cm), a 260% increase in distance. See Figure 5.1 for an aviary schematic showing O and F locations.

Table 4. Conditions for Experiment 3

Condition	Dates 2003	Length
Single Camera View: Bowl & Bath (time-lapse recording)		
Baseline	Apr 28 - May 12	2 weeks
Reintroduction (Condition A)	May 12 – May 26	2 weeks
Bowl: original location		
Tools: Frisbee, Cup, Ring		
Will a relearning period be necessary for Frisbee and Cup to be used as food and water portage tools?		
Single Camera View: Bowl Close-up (time-lapse recording)		
Condition B	May 26 – Jul 14	7 weeks
Bowl: Far		
Tools: Frisbee, Cup, Ring		
Will increasing the distance between food and water produce a decrease or cessation of water deposits into the bowl?		
Condition C	Jul 14 – Jul 28	2 weeks
Bowl: Far		
Tools: Cup, Ring		
Will water deposits to the bowl resume after the removal of the preferred tool (Frisbee)?		
Condition D	Jul 28 – Aug 11	2 weeks
Bowl: Original		
Tools: Cup, Ring		
Will water deposits to the bowl resume after the removal of the preferred tool (Frisbee) and the bowl is returned to its original location?		
Condition A2	Aug 11 – Aug 25	2 weeks
Bowl: Original		
Tools: Frisbee, Cup, Ring		
Will water deposits to the bowl resume after all tools are reinstated and the bowl is returned to its original location?		
Two Camera Views: a Bowl Close-up (real-time recording) and an Aviary Overhead view (time-lapse recording)		
Condition A3+	Aug 25 – Sep 8	2 weeks
Bowl: Original		
Tools: Frisbee, Cup, Ring		
Condition B2+	Sep 8 – Sep 22	2 weeks
Bowl: Far		
Tools: Frisbee, Cup, Ring		
When water and food are acquired but not transported to the bowl and bath, where are they being taken?		

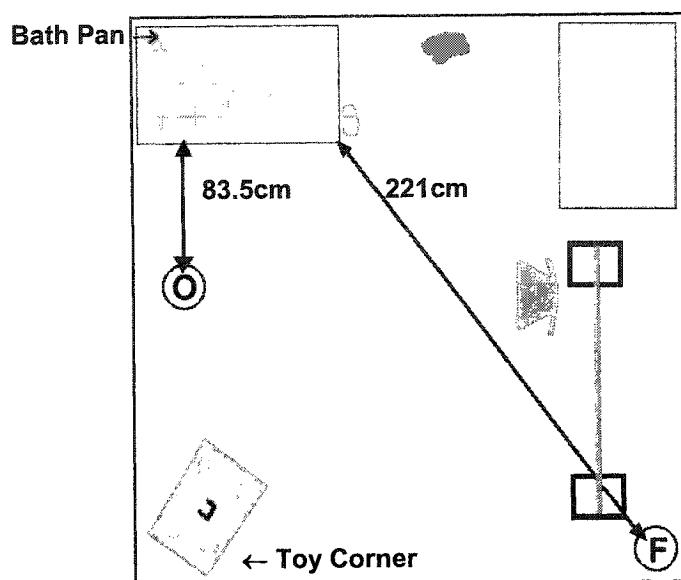


Figure 5.1 A schematic of the aviary layout for the Experiment 3 conditions. Two possible locations for the food bowl are denoted: “O” is the original location, and “F” is the farthest possible location from the water source.

Data Collection

Real-Time Observation

The video and audio signals from both the CCTV and the camcorder were routed to a nearby room, through a switcher and then to a color monitor. This provided a venue for remote real-time observation that allowed an observer to switch between the overhead and close-up views. At least one trained observer was near the monitor each day during the aviary’s light phase (8:00am – 8:00pm). Most of Loki’s activities produced very distinct sounds, and these sounds easily alerted the observer to pay attention and make notes regarding activities at the bath or bowl.

Time-Lapse Recording

For baseline and the first five conditions (A, B, C, D, A2), the video and audio signals from the Sony camcorder (bowl area) were also sent to a Panasonic time-lapse video recorder (model AG6730) that recorded continuously throughout the aviary's light phase (5 frames per second/12 hours per day).

For the last two conditions (A3+, B2+), the bowl area was recorded in real-time rather than time-lapse using Sony VHS videocassette recorders (model SLV-N500), and the overhead CCTV view was routed to the Panasonic time-lapse video recorder (model AG6730). Thus both the bowl area (real-time VHS) and the entire aviary (time-lapse, 5 frames per second) were recorded continuously throughout the light phase for the last two conditions

Videotapes were reviewed to determine the frequency and manner of use of the reintroduced objects.

Results

Baseline

No forms of tool use involving water or food portage were seen occurring at the bowl or bath during the baseline period.

Condition A

During the first few hours of Condition A, both the Frisbee and cup were used to carry food and water respectively (see Table 5).

Table 5. Tool Reintroduction Results

Time	Behavior	Post-reintroduction Latency
2:47PM	Food bowl made available	
2:55PM	GC, GR, FR and other toys made available	
3:14PM	Loki looks at the toy pile	19min
4:08PM	FR deposited into bowl, flipped, placed on floor, placed back in bowl and flipped, placed on floor and left there	73min
4:20PM	FR used to transport food to water	85min
5:42PM	FR used to transport food away (off camera)	167min
6:29PM	GC used to acquire and deliver water from the bath into the bowl	214min

The remaining data for the two weeks in which Condition A was in effect showed that the Frisbee was used to transport chow to the Bath with a weekly mean frequency of $\bar{X} = 3.00$, $sd = 3.00$. All means reported in this section represent mean weekly frequencies (sd = standard deviation). The cup was used to acquire and transport water to the bowl more often, and with more consistency ($\bar{X} = 9.50$, $sd = 0.50$).

Conditions B, C, D and A2

Water deliveries to the bowl stopped abruptly once it was moved to the far corner of the aviary and did not resume for the entire seven weeks of Condition B. However, use of the Frisbee to scoop up and transport chow away from the bowl increased to many times per week ($\bar{X} = 12.14$, $sd = 8.53$).

Water deliveries to the bowl did not resume during Condition C, in which the Frisbee was made unavailable and the bowl remained in the distant location,

or during Condition D, in which the Frisbee remained unavailable and the food bowl was relocated back to its original position. Once the Frisbee was returned to the aviary (Condition A2) it was again used to transport chow away from the bowl ($\bar{X} = 4.50$, $sd = 2.50$), while water deliveries to the bowl using the cup continued to be nonexistent.

Conclusions

From these data it seems that once the bowl was moved away from the water (Condition B), moving food with the Frisbee became a preferred activity over moving water to the bowl with the Cup. Unfortunately, the camera set-up in Conditions B, C, D, and A2 did not allow for determinations regarding where the food was going, only that it was being taken away from the bowl, presumably to the bath. Without more information on where the food was going it cannot be determined if, in the wake of a dramatic change, Loki reverted to his first form of tool use, thus making the food hauls compensatory actions, or if the food was now being taken to non-bath locations as well. Loki's behavior from the earliest condition (A) showed that he did occasionally transport chow via the Frisbee to locations other than the bath (off-camera $\bar{X} = 1.50$, $sd = 0.50$), but its most common destination was still the bath ($\bar{X} = 3.00$, $sd = 3.00$). An indulgence in extrapolation would suggest that it is likely that most of the food portage in Condition B ended up at the bath. Additional data from the daily aviary inspections fortify this supposition, as chow was never found in any location except for the bowl. Once the bowl was moved to the far location and Loki

ceased to carry water to it, he may still have been moistening his food by carrying food to the bath using the Frisbee. It is curious that Loki did not continue water portage to the bowl. Rather than providing an unambiguous answer to the original efficiency versus play question, these results generate additional questions regarding factors that affect tool preference.

Further data from Condition A also showed that water was transported most often *not* to the Bowl ($\bar{X} = 9.50$, $sd = 0.50$) but off camera ($\bar{X} = 14.00$, $sd = 3.00$). The portage of water to non-bowl destinations was also reported in the post-experimental data for Chapter 4. To determine where the food and water were being taken, additional video recorders were acquired and Conditions A3+ and B2+ were conducted.

Conditions A3+ and B2+

In Condition A3+, with all tools available and the bowl in its original location, Loki used the Frisbee to transport chow to the bath only about once a week ($\bar{X} = 1.00$, $sd = 1.00$). He used the Frisbee to transport chow to other locations in the aviary with even less weekly frequency ($\bar{X} = 0.50$, $sd = 0.50$). He also made very few water deliveries weekly to the bowl using the Cup ($\bar{X} = 1.50$, $sd = 0.50$). However, water deliveries to other areas in the aviary continued to occur often ($\bar{X} = 21.50$, $sd = 8.50$).

For the last condition (B2+, for which the bowl was again moved to the far location), Frisbee food portage to the bath ($\bar{X} = 0.50$, $sd = 0.50$) and to non-bath locations ($\bar{X} = 1.50$, $sd = 0.50$) continued to occur infrequently and water

deliveries to the bowl using the cup did not occur at all. However, water deliveries to non-bowl destinations continued to occur often ($\bar{X} = 21.00$, $sd = 13.00$). The weekly mean frequencies of food and water portage, using Frisbee and cup respectively, during the last two conditions (A3+ and B2+) can be seen in Figure 5.2. Data from Condition A are also included for comparison purposes. Data were not available from Condition A regarding where the non-bowl water deliveries were destined. However, the overhead camera views recorded during Conditions A3+ and B2+ revealed that water deliveries were destined to seven general locations within the aviary. These can be seen in Figure 5.3.

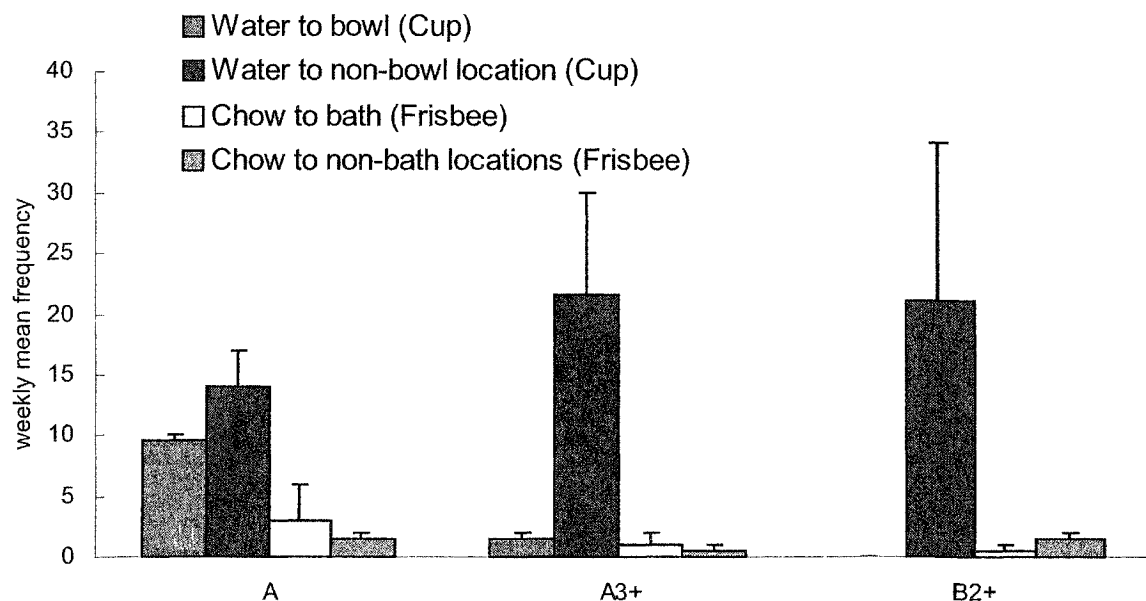


Figure 5.2 A comparison of the mean weekly frequency (SD) of cups of water that were delivered into the bowl or off camera, as well as chow deliveries using the Frisbee that went to the bath or off camera, for the three conditions where all tools were available.

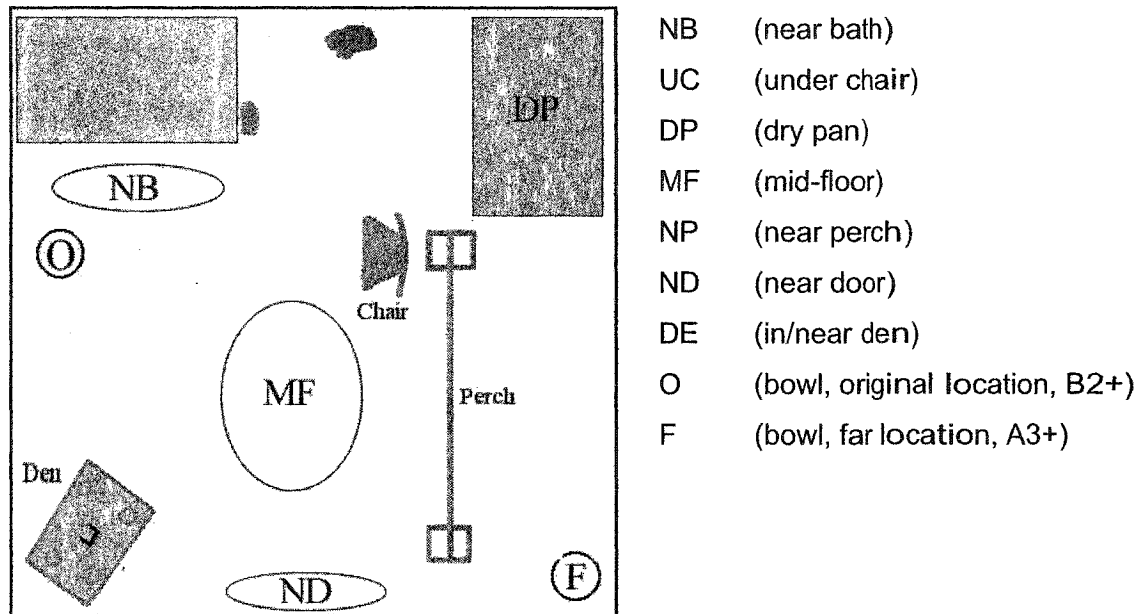


Figure 5.3 A schematic (not to scale) of the aviary denoting the general locations where water deliveries occurred during Conditions A3+ and B2+.

Neither the weekly rate of water deliveries to all non-bowl locations for the last two conditions (Figure 5.2), nor the rate of delivery to each of the different locations (Figure 5.4) appeared to have a systematic relationship to where the bowl was located.

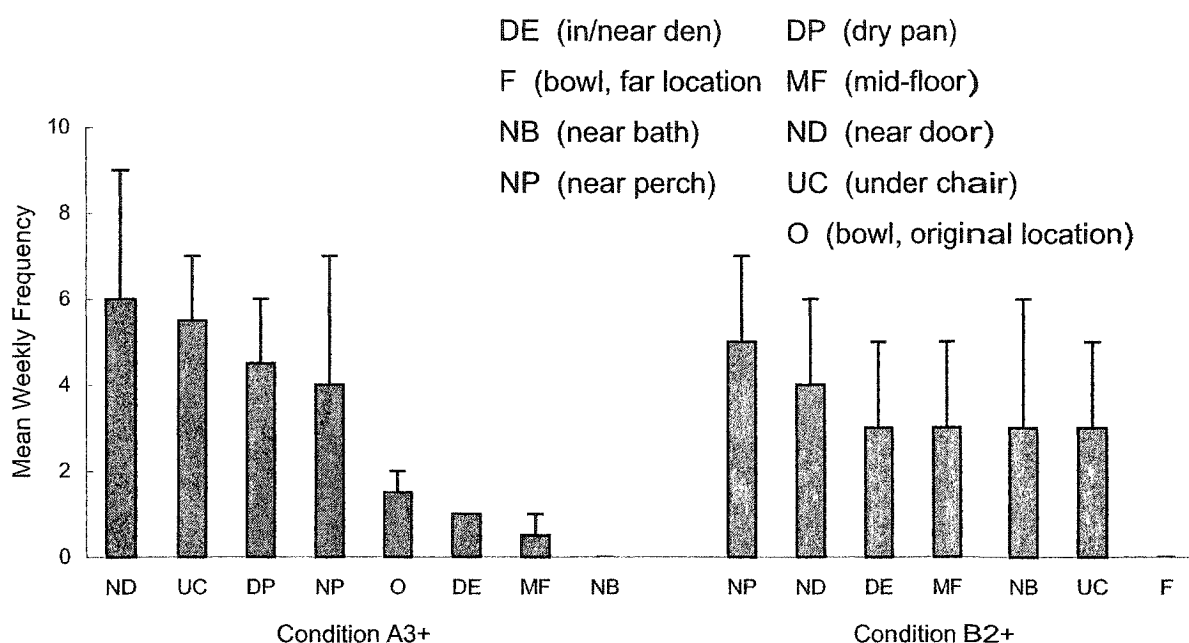


Figure 5.4 The mean weekly frequency (SD) of water deliveries to various locations in the aviary for Conditions A3+ and B2+ arranged in descending order.

General Conclusions

When the Frisbee and cup were returned to the aviary after their long absences, Loki used them both to acquire and deliver food and water to the bath and bowl respectively within hours of their return. However, once the bowl was moved to the more distant location, water deliveries to it abruptly stopped and food portage using the Frisbee increased (Condition B). It appeared that, under these new circumstances, the Frisbee became the preferred tool and food portage became the preferred food-related tool use act. Food portage using the Frisbee increased and remained at relatively high levels for the remaining 4 weeks of that condition (Condition B). Unfortunately restricted camera-views

meant that it could not be determined whether those food hauls were all destined for the bath, and thereby functioning as compensatory acts, or whether food was being taken to places other than the bath.

Surprisingly, even when the Frisbee was removed (Condition C) and the bowl returned to its original location (Condition D) water portage to the bowl did not resume. It did, however, recommence after the bowl had remained in its original location and all tools were available for 3 weeks (Condition A2 and A3+), but only at very low rates, with a cup of water being poured into the bowl only about once a week. Water portage to the bowl stopped again when the bowl was moved back to the more distant location during the final condition (B2+). The moving of the bowl back and forth between the two possible locations did have an effect on water-portage behavior, though that effect was not as straightforward as hoped.

The high initial rates of water portage to the bowl seen in Condition A could have been a novelty effect. About 15 months had passed since Loki had the opportunity to engage in this unique form of food soaking, given the absence of the cup from the aviary. The cessation of water portage to the bowl after its first repositioning suggested that water deliveries to the bowl were indeed affected by the bowl's distance from the water, but why the behavior was affected remains unclear. Perhaps it was because such trips required more energy than they were worth, as suggested earlier. Support for this interpretation could have been found if water portage to the bowl had recommenced when it was positioned back at its original location, but that did not happen.

Perhaps moving the bowl put the room in a new configuration, which was enough of a novelty itself to disrupt the relatively more familiar behaviors. But why did other behaviors recover and even increase (Frisbee food portage), while water portage remained conspicuously absent? Perhaps something else was being learned about water portage during that time.

Neither water portage to the bowl nor food portage to the bath were systematically controlled by the distance of the bowl from the water or the absence of the Frisbee. Therefore the question of whether Loki's bowl-directed water portage reflected acts of energy efficiency or play was not clearly answered by this study.

Given that there are no explanations for why Loki, or any other crow, moistens or washes food before consuming it, we can only postulate the function food-wetting serves (e.g., an aid to palatability, digestibility or exploitability). And given that Loki, as well as free-living crows, often consumes dry food without the benefit of soaking or washing, we must assume that under most circumstances food wetting is non-essential. This rather calls into question the value of knowing whether Loki's bowl-directed water-portage constitutes an efficient behavior or play. It is still tool-use, *regardless* of its function.

Nevertheless, there is an epilogue and a final supposition. Since the last condition in this experiment Loki has had continued access to both Frisbee and cup, and the food bowl has remained in its original location. Even so, at the time of this writing, water has been found in the bowl only twelve times (September 8, 2003 – August 31, 2004). So water portage to the bowl has *still* not resumed as

a regular occurrence, even after nearly 12 months. In contrast, Loki continues to use the Frisbee for food portage to the bath, and to engage in two pre-tool behaviors: carrying chow in his beak to the bath and eating dry chow directly from the bowl. And, of course, he still uses the cup to acquire water and make puddles in other areas of the aviary. Relatively speaking, water portage to the bowl has now become a rare occurrence.

In conclusion, if Loki's water deliveries to the bowl were indeed, all along, acts of play rather than efficiency, it could be that the increase in distance between the bowl and the water disrupted the playful behavior long enough to make conditions favourable for Loki's return to the more natural, first-learned, behavior of food portage to the water by beak and Frisbee. Certainly the clearest conclusion produced by this experiment is that further research will be necessary to elucidate the relationship between play and efficiency for Loki's water deliveries to the bowl.

Chapter 6

General Discussion

Over the course of this six-year study Loki exhibited five kinds of tool use involving five different objects:

Water Acquisition & Portage	Frisbee, Nozzle, Cup
Food Acquisition & Portage	Frisbee
Food Portage	Cup
Object Portage	Frisbee, Cup
Head Scratching	Slinky
Microphone Access	Perch

Water Portage with The Cup

As mentioned earlier, the use of hollow vessels to contain and transport water, or anything else, is a rare form of tool use. Reports for primates consist almost entirely of those of captive chimpanzees for which the behavior developed only after observing humans¹⁸. Hess's crow (as reported in Beck, 1980) could also have learned to acquire and transport water imitatively. However, in Loki's case, this was not a possibility. The cup, as well as the Frisbee and nozzle, were never used as portage tools by anyone but Loki. Furthermore, the study reported in Chapter 1, as well as the observational data collected over the five subsequent years, provided no evidence for movement imitation with or without objects. Certainly, evidence of absence in an individual does not constitute evidence of absence for the species. But in this case, it does constitute evidence that

¹⁸ The use of leaf sops, crumpled and/or chewed leaves to acquire water from otherwise inaccessible locations, has been reported in free-living chimpanzee groups. Sops may function to acquire water from a tree depression and get it quickly to the mouth, but would not suffice to transport water any distance. The term *portage tool* has been introduced to differentiate a tool used to contain and transport from a tool used merely for acquisition. Tools that function acceptably for one job may not be sufficient for the other.

imitation was not required for the development of the specific tool use acts reported here, some of which were extraordinarily complex.

Food and Water Portage with the Frisbee

Loki began depositing inedible items into the bath at an early age (around four weeks of age, see Chapter 2). His initial placement of these objects into the water appeared to have no purpose, but speculatively could have been related to species-common food-soaking behavior. But why would one go from such a natural behavior as soaking food to such an apparently unnatural behavior as soaking inedible objects. One possibility is that with some soaking, they *might* become edible.

Items that seem inedible because they are hard may become edible when waterlogged. Therefore taking apparently inedible items to water might result in the exploitation of a new food source. For example, Loki was given hard, dry dog biscuits. His standard procedure was to deposit them into the water pan and, with this treatment, they quickly become soft and easily edible. Brazil nuts were also occasionally provided. These nuts are particularly difficult to crack, so difficult in fact that Loki never managed to open a single one on his own. Ones that were provided to him partially cracked were always neatly consumed. However, each nut that was provided whole was soaked repeatedly in the water pan, sometimes for several days. Regardless, Loki never succeeded in cracking a Brazil nut on his own. The soaking of an apparently inedible object sometimes pays off, and sometimes it does not. But if one is provisioned well enough that hunger isn't an immediate priority, it is worth a try.

It is unfortunate that we have no record regarding where the Frisbee went first, into the water pan or into the food bowl. Subsequent observations of Loki's behavior with new objects (e.g., the cup, Chapter 4, and P.D. Cole, unpublished data) have shown that he invariably placed them first in the food bowl, sometimes pushing them deeply under the food, hours and often days before they were introduced into the water pan. Operating under the assumption that this too occurred with the Frisbee, it is possible that a deep caching of the Frisbee, and its subsequent recovery produced the first serendipitous portage of food to water. Thus, under certain circumstances, the Frisbee did indeed become edible, or at least, it produced edible bits.

Repeated combinations of caching and soaking, maintained through Thorndikian conditioning, could have increased the likelihood of recurring trips from bowl to bath. The return trips, which introduced water into the bowl and allowed for the consumption of moist chow right at the bowl, were also reinforcing and thereby increased the likelihood that the Frisbee would be repeatedly returned to the food bowl, once it had been "soaked".

The combined effects of caching, soaking and Thorndikian conditioning provide one possible explanation as to how Loki's Frisbee portage-behavior came to be. But it does not offer any explanation for the skillful flipping manipulation that Loki developed at the bowl, to get water off, and food onto, the Frisbee.

Foraging crows are known to flip over leaves and rocks, and when in pastures, cowpats. This may serve two purposes, the discovery of live edibles

underneath (Kilham, 1989), or the recovery of food previously cached, either by oneself, or by another. Kilham described free-ranging American Crows on a farm in Florida spending a great deal of time foraging under cowpats: “A usual approach was to seize a cow pie, push it up on edge, then let it fall over” (1989, p.16). This accurately describes Loki’s early Frisbee manipulations at the bowl. A drawing in Kilham’s book also shows a crow standing on top of a dried cowpat (p.54). Loki often stood on the Frisbee as well, and only when the concave side was down.

This is not to say that cowpat-directed behavior, specifically, is innate; rather, that objects of a certain size and shape may initially elicit specific, though modifiable behaviors, which provide the bases for more refined behaviors. Thus, after placing (caching) the Frisbee in the bowl, Loki would have had to move it to access the food underneath. Grasping and edging the Frisbee over like a cowpat might have placed the Frisbee, still inside the bowl, with the concave side upright and bearing chow. Thorndikian conditioning could then have served to refine the flipping motion into a slightly more refined scooping action.

Perch Moving

Moving the tripod-perch under the microphone is reminiscent of the behavior exhibited by some of Köhler’s chimpanzees. The chimp’s behavior prompted Köhler to propose insight as the underlying learning mechanism. But Loki manipulated everything in the aviary (Chapter 3). He seemed especially attracted to small, black objects (the plastic wing-nuts on the dog den; the knob on the weight scale), and the tripod had soft, black, removable, rubber coverings

on its feet (see Figure B1, Appendix B). Loki had been steadily removing small bits of rubber from the feet by pecking, ripping and pulling for several months after the initial introduction of the perch. The tripod had been found slightly repositioned, though never by more than a few inches, several times prior to the day on which the incident reported in Chapter 3 occurred. Thus, as thoughtful as Loki's perch-moving might have appeared, it was perhaps nothing more than the result of a sustained bout of pecking and pulling at the rubber coverings on the feet of the tripod which caused it to serendipitously end up under the microphone.

Slinky Head-Scratcher

The most complex sequence of tool behavior involved the Slinky. Loki often took food and non-food items up to the perch, where he cached them in the "Y" of the perch or, in the case of the PVC ring (Appendix B, Figure B3), threaded it over the vertical perch support. During the early days of its availability, the Slinky was also taken up to the perch, and pressed onto the branch part of the perch itself, where it wedged fairly securely. As stated in Chapter 1, crows seem compelled to pull at rope- or string-like materials (including the tails of dogs and cats, and in the case of ravens, wolves). A small imaginative stretch could also envision a crow or raven pulling entrails from a carcass, or small snake-like prey from their hiding places. Perhaps this species-typical behavior is what initially prompted Loki to begin pulling on the free end of the suspended Slinky. After 11 months of more and then less rambunctious tugging, some approaches to the

swinging Slinky could have resulted in accidental, though reinforcing, head rubs, which operant conditioning and perhaps skill learning served to refine.

Toy Portage

Placing or wedging inedible objects into crevices or receptacles is a common behavior not only among American Crows (P.D. Cole, personal observations), but also the New Caledonian Crow (J. Chappell, 2002, personal communication). Anecdotal reports abound of wild crows hiding found objects such as jewellery, silverware, and marbles in holes they have dug in flowerpots, gardens, and so on. This appears to be a form of caching which has generalized beyond food to attractive items. Reid's (1982) explanation of the captive rook's tool use that resulted in pools of water (Chapter 1, Table 1) relied upon caching directed at a non-food item (a *black*, rubber stopper), which was reinforced by the formation of the pool of water. In Loki's case, the cup was treated like a portable cache. It was sometimes found with food and non-food objects inside, neatly obscured by wads of paper towel pressed on top.

Object-Directed Play

Most of Loki's object interactions along the way to tool use appeared, pragmatically, to be unnecessary. Beck (1980) proposed that differences, both phyletic and perhaps even individual, in the occurrence of learned tool behavior are largely subject to "variations in the predisposition to fiddle with objects, as well as morphological capabilities, and in the capacity to learn."

This "predisposition to fiddle with objects" is also often referred to as *object-directed play*. This type of play has been traditionally proposed as one

way in which individual animals learn about the characteristics of things, knowledge that may not be immediately applicable but may become useful later, and as such can function as a precursor to tool use. (One example of Loki engaging in object-directed play that eventually led to the headscratching behavior can be seen in DV10, Appendix D). No general consensus has been reached regarding an operational definition for play¹⁹, so for present purposes the discussion of play will be restricted to object-directed behaviors that appear to serve no subsistence-related purpose.

Play is often seen only in juveniles. However, Loki's interaction with all kinds of inedible objects has persisted into his adulthood (P.D. Cole, unpublished data). Interactions with new objects may function as exploration, but Loki's continued interactions with familiar items, some of which he has had near-daily access to for 4 years or more, appears to be play for the sake of play (true play). (For some examples of Loki's object-directed activities that appear to be true play, see DV11 – DV18, Appendix D).

Corvids, even more than parrots (Diamond & Bond, 2003), are reported to engage in playful behavior involving objects (Fagen, 1981; Ficken, 1977; Ortega & Bekoff, 1987), and Loki was raised in an environment that was especially conducive to play. His subsistence needs - water, food, shelter, safety - were all provided for and he spent a fair amount of time alone²⁰. He was introduced to small, colorful objects early in his life, and he saw humans interacting with

¹⁹ Fagen's now classic *Animal Play Behavior* (1981) provides a list of about 40 definitions.

²⁰ Captive, Hawaiian crows (*Corvus hawaiiensis*), isolate-reared during their first year, are reported to engage more often in play-like behavior than those that have been group-reared (Harvey, Farabaugh, & Druker, 2002).

objects (stimulus enhancement) every day²¹. The propensity to approach and interact with inanimate, inedible, objects may have been the most important genetic determinant of the development of Loki's innovative tool use²².

Object-directed play that continues to occur throughout adulthood may be indicative of more than exploration. These behavioral patterns may now be play simply for the sake of play (true play). In these cases, the reinforcement may not be as tangible as it is in the other cases, but the acts might still qualify as tool use.

Object-Directed Play as Tool Use

Tool use acts are often considered so because they appear to be subsistence related. But, for example, the use of leaf sops occurs under "unnecessary" circumstances. Goodall reported observing eighteen instances of chimpanzees using leaf sops at streams, where the water was readily available for drinking (1986). Even Köhler admonished care when interpreting behavior that involves objects, as it might be closer to play than problem solving.

Kitahara-Frisch went on to suggest that much of the tool use behavior reported in

²¹ It should be stressed that none of Loki's tool use behaviors have occurred while humans were present in the aviary. They have only been witnessed through CCTV cameras and videotape. This should answer the question of whether social reinforcement played a role in the development of specific tool use acts. However, social reinforcement probably did encourage Loki's interactions with three specific objects and perhaps all other objects in a more general way. After Experiment 1 was completed, two social + object games were introduced: catch (food → yellow lid → Frisbee) and toss (white practice golf ball and green wiffle ball). These games are described in Appendix C. Aside from the modeled behaviors described for Experiment 1, the two social + object games, and the ritualized daily cleaning, the Experimenter did not use any of the other enrichment objects in any other way.

²² Even in the woodpecker finches, a period of playful manipulation was proposed as a necessary ontogenetic component leading to the species-specific act of using twigs as probes (Tebich et al., 2001).

the East African wild chimpanzees could be better understood as manifestations of play (1977). Presumably for Köhler, Kitahara-Frisch, and for many others, an act must be subsistence-oriented to justify being called “tool use”. But Beck reported that captive primates that have acquired a tool use behavior will often perform these acts in the absence of any incentive, suggesting that some species may find the process of using tools as rewarding as the incentives (1980, p.152). Furthermore, and with the understanding that Beck might not agree with ensuing, his definition of tool use does allow for the alteration of “the condition ... of the user itself”. Therefore object-directed play, under some circumstances, could be considered tool use.

Some of Loki’s object-directed play was essential to the development of his tool use and therefore fulfilled the role of object-directed play as object exploration. But he also engaged in many other object-directed behaviors, which often consisted of the combining and recombining of objects, and which persisted long after their characteristics should have become familiar. Therefore these behaviors should also be considered tool use, although with less tangible benefits than the other tool use acts documented in this study.

Huffman & Quiatt (1986) reported the results of a near 10-year study of stone handling in free-roaming Japanese Macaque (*Macaca fuscata fuscata*), from its sudden appearance (innovation) in a single individual to its transmission throughout the group. Contrary to all other newly acquired behavior reported for this group, stone handling is not subsistence-oriented, and appears to provide no tangible benefits to the handler. Huffman suggested that stone handling may be

relaxing or stimulating, thus the benefits would be physiological or psychological, and therefore undetectable to the casual human observer.

In summary, object-directed play as an act of tool use, rather than object exploration, could be characterized as a learned object-directed behavior that persists after object-familiarity is gained; the benefits of which may not be apparent but must be considered self-evident by the animal's continued engagement in the act.

Innovative Tool Use

In his discussion of the ontogeny of tool use, Beck advised that the “discovery”²³ of a tool use behavior could be considered to have occurred either when an isolated animal acquires a form of tool use behavior for the first time, or when a group-living animal acquires a tool use form that is novel within its social group. Beck also advised that to document scientifically the origin of the behavior “the history of the animal must be known sufficiently to conclude that it has never before performed the tool behavior in question or observed the behavior performed by others” and that “the very first performance must be observed and documented to illuminate the dynamics of acquisition”. At the time of his book, he concluded that “no case of the discovery of tool behavior that meets all of these requirements is known” (Beck, 1980). Given the present results, the last statement is no longer accurate. The tool use behaviors documented were certainly innovative, the history of the animal was well known, and the first instances of cup use were documented.

²³ The use of *discovery* is here considered synonymous with *innovation*.

Closing Thoughts

The development of complex sequences from relatively simple components is ubiquitous in nature, and the development of Loki's tool use was no exception. The manipulation of inanimate objects is prevalent in corvids and Loki spent long hours repeatedly manipulating every unattached object (and even some attached objects) in the aviary. Some of those activities produced explicitly or implicitly satisfying outcomes -- in which cases, instrumental learning (Thorndikian and operant conditioning, and skill learning) served to increase the likelihood of their occurrence, and to fine-tune the numerous components of each act. Over the months, the various forms of object manipulation and learning were slowly chained together, thereby producing Loki's increasingly complex behavior, and eventually culminating in complex acts of tool use.

Explanations like those proposed here, which do not rely upon miracles, magic, or metacognition, may seem to take all the fun out of the study of tool use behavior. But it need not. The crow is an impressive creature that will always engage our imaginations with enigmatic acts. Perhaps the production of complex acts of tool-use, achieved via the modification of species-typical behaviors and relatively simple, but powerful, associative learning mechanisms, is his most elegant trick of all.

References

- Antevs, A. (1948). Behavior of a gila woodpecker, ruby crowned kinglet, and broad tailed hummingbird. *Condor*, 50, 91-92.
- Balda, R. P., & Kamil, A. C. (1989). A comparative study of cache recovery by three corvid species. *Animal Behaviour*, 38(3), 486-495.
- Balda, R. P., & Kamil, A. C. (1992). Long-term spatial memory in Clark's nutcracker, *Nucifraga columbiana*. *Animal Behaviour*, 44(4), 761-769.
- Beck, B. B. (1974). Baboons, chimpanzees and tools. *Journal of Human Evolution*, 3, 509-516.
- Beck, B. B. (1980). *Animal tool behavior : the use and manufacture of tools by animals*. New York: Garland STPM Publishing.
- Bednekoff, P. A., Balda, R. P., Kamil, A. C., & Hile, A. G. (1997). Long-term spatial memory in four seed-caching corvid species. *Animal Behaviour*, 53(2), 335-341.
- Boswall, J. (1977). Tool-using by birds and related behaviour. *Avicultural Magazine*, 83, 88-97, 146-159, 220-228.
- Boswall, J. (1978). Further notes on tool-using by birds and related behaviour. *Avicultural Magazine*, 84, 162-166.
- Boswall, J. (1983a). Tool-using and related behaviour in birds: more notes. *Avicultural Magazine*, 89, 94-108.
- Boswall, J. (1983b). Tool-using and related behaviour in birds: yet more notes. *Avicultural Magazine*, 89, 170-181.
- Brooke, R. K. (1979). Predation on Ostrich eggs by tool-using crows and Egyptian Vultures. *Ostrich*, 50, 257-258.
- Caffrey, C. (2000). Tool modification and use by an American Crow. *The Wilson Bulletin*, 112(3), 283-284.
- Chance, M. R. A. (1960). Kohler's Chimpanzees-How Did They Perform? *Man*, 60, 130-135.
- Chappell, J., & Kacelnik, A. (2002). Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*). *Animal Cognition*, 5(2), 71-78.

- Clayton, N. S., & Dickinson, A. (1999a). Memory for the content of caches by scrub jays (*Aphelocoma coerulescens*). *Journal of Experimental Psychology: Animal Behavior Processes*, 25(1), 82-91.
- Clayton, N. S., & Dickinson, A. (1999b). Motivational control of caching behaviour in the scrub jay, *Aphelocoma coerulescens*. *Animal Behaviour*, 57(2), 435-444.
- Cook, M., & Mineka, S. (1990). Selective associations in the observational conditioning of fear in rhesus monkeys. *Journal of Experimental Psychology: Animal Behavior Processes*, 16(4), 372-389.
- Curio, E., Ernst, U., & Vieth, W. (1978). Cultural transmission of enemy recognition: One function of mobbing. *Science*, 202(4370), 899-901.
- Diamond, J., & Bond, A. B. (2003). A comparative analysis of social play in birds. *Behaviour*, 140(8-9), 1091-1115.
- Duerden, J. (1905). On the habits and reactions of crabs bearing actinians in their claws. *Proceedings of the Zoological Society of London*, 2, 494-511.
- Fagen, R. M. (1981). *Animal Play Behavior*. New York: Oxford University Press.
- Fellers, J., & Fellers, G. M. (1976). Tool use in a social insect and its implications for competitive interactions. *Science*, 192(4234), 70-72.
- Ficken, M. S. (1977). Avian Play. *The Auk*, 94, 573-582.
- Goodall, J. (1986). *The chimpanzees of Gombe : patterns of behavior*. Cambridge, Mass.: Belknap Press of Harvard University Press.
- Harvey, N. C., Farabaugh, S. M., & Druker, B. B. (2002). Effects of early rearing experience on adult behavior and nesting in captive Hawaiian crows (*Corvus hawaiiensis*). *Zoo Biology*, 21(1), 59-75.
- Huffman, M. A., & Quiatt, D. (1986). Stone handling by Japanese macaques (*Macaca fuscata*): Implications for tool use of stone. *Primates*, 27(4), 413-423.
- Hunt, G. R. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature*, 379, 249-251.
- Hunt, G. R. (2000). Tool use by the New Caledonian Crow *Corvus moneduloides* to obtain Cerambycidae from dead wood. *Emu*, 100(2), 109-114.
- Hunt, G. R., Corballis, M. C., & Gray, R. D. (2001). erratum: Laterality in tool manufacture by crows. *Nature*, 415(6872).

- Hunt, G. R., & Gray, R. D. (2002a). Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proceedings of the Royal Society of London B*.
- Hunt, G. R., & Gray, R. D. (2002b). Species-wide manufacture of stick-type tools by New Caledonian Crows. *Emu*, 102(4), 349-353.
- Janes, S. (1976). The apparent use of rocks by a raven in nest defense. *Condor*, 78, 409.
- Jewett, S. C. (1924). An intelligent crow. *Condor*, 4, 14.
- Kamil, A. C., & Balda, R. P. (1985). Cache recovery and spatial memory in Clark's nutcrackers (*Nucifraga columbiana*). *Journal of Experimental Psychology: Animal Behavior Processes*, 11(1), 95-111.
- Katz, D. (1937). *Animals and men.*: Longmans, Green.
- Kilham, L. (1968). Reproductive behavior of white-breasted nuthatches. I. Distraction display, bill-sweeping, and nest hole defense. *Auk*, 85, 477-492.
- Kilham, L. (1971). Use of blister beetle in bill-sweeping by white-breasted nuthatches. *Auk*, 88, 175-176.
- Kilham, L. (1989). *The American crow and the common raven.*: College Station : Texas A&M University Press, c1989.
- Kitahara-Frisch, J. (1977). Tools or Toys? What have we really learned from wild chimpanzees about tool use? *Journal of the Anthropological Society of Nippon*, 85(1), 57-64.
- Köhler, W. (1927). *The mentality of apes* (E. Winter, Trans. 2nd ed.). New York: Harcourt, Brace.
- Lefebvre, L., Nicolakakis, N., & Boire, D. (2002). Tools and brains in birds. *Behaviour*, 139(7), 939-973.
- McGrew, W. C. (1992). *Chimpanzee material culture: Implications for human evolution.*: Cambridge University Press.
- Moore, B. R. (1992). Avian movement imitation and a new form of mimicry: Tracing the evolution of a complex form of learning. *Behaviour*, 122(3-4), 231-263.
- Moore, B. R. (1996). The evolution of imitative learning. In C. M. G. Heyes, Bennett G. Jr. (Ed.), *Social learning in animals: The roots of culture*. (pp. 245-265). San Diego, CA, US: Academic Press, Inc.

- Moore, B. R. (2004). The Evolution of Learning. *Biological Review*, 79, 301-335.
- Orenstein, R. I. (1976). Tool-use by the New Caledonian Crow (*Corvus moneduloides*). *Auk*, 89, 674-676.
- Ortega, J. C., & Bekoff, M. (1987). Avian play: Comparative evolutionary and developmental trends. *Auk*, 104(2), 338-341.
- Owings, D. H., & Coss, R. G. (1977). Snake mobbing by California ground squirrels: Adaptive variation and ontogeny. *Behaviour*, 62(1), 50-69.
- Porter, J. P. (1910). Intelligence and imitation in birds: A criterion of imitation. *American Journal of Psychology*, 21(1), 1-71.
- Povinelli, D. J. (2003). Folk physics for apes: The chimpanzee's theory of how the world works. *Human Development*, 46(2), 161-168.
- Povinelli, D. J., & Vonk, J. (2003). Chimpanzee minds: Suspiciously human? *Trends in Cognitive Sciences*, 7(4), 157-160.
- Povinelli, D. J., & Vonk, J. (2004). We don't need a microscope to explore the chimpanzee's mind. *Mind & Language*, 19(1), 1-28.
- Powell, R. W., & Kelly, W. (1975). A method for the objective study of tool-using behavior. *Journal of the Experimental Analysis of Behavior*, 24(2), 249-253.
- Powell, R. W., & Kelly, W. (1977). Tool use in captive crows. *Bulletin of the Psychonomic Society*, 10(6), 481-483.
- Powell, R. W., Kelly, W., & Santisteban, D. (1975). Response-independent reinforcement in the crow: Failure to obtain autoshaping or positive automaintenance. *Bulletin of the Psychonomic Society*, 6(5), 513-516.
- Rajan, & Balasubramanian. (1989). Tool-using behavior in Indian House Crow *Corvus splendens*. *Journal of the Bombay Natural Historical Society*, 86, 450.
- Reid, J. B. (1982). Tool-use by a rook (*Corvus frugilegus*) rook (*Corvus frugilegus*), and its causation. *Animal Behaviour*, 30(4), 1212-1216.
- Russon, A. E., & Galdikas, B. M. (1993). Imitation in free-ranging rehabilitant orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology*, 107(2), 147-161.
- Rutledge, R., & Hunt, G. R. (2004). Lateralized tool use in wild New Caledonian crows. *Animal Behaviour*, 67(2), 327-332.

- Schiller, P. H. (1957). Innate motor action as a basis of learning: manipulative patterns in the Chimpanzee. (C. H. Schiller, Trans.). In C. H. Shiller (Ed.), *Instinctive Behavior*. New York: International Universities Press, Inc.
- Sherry, D. F., & Galef, B. G. (1984). Cultural transmission without imitation: Milk bottle opening by birds. *Animal Behaviour*, 32(3), 937-938.
- Sherry, D. F., & Galef, B. G. (1990). Social learning without imitation: More about milk bottle opening by birds. *Animal Behaviour*, 40(5), 987-989.
- Sibley, C. G., & Monroe, B. L. (1990). *Distribution and taxonomy of birds of the world.*: New Haven : Yale University Press.
- Sibley, C. G., & Monroe, B. L. (1993). *A Supplement to Distribution and Taxonomy of Birds of the World.*: New Haven: Yale University Press.
- Spence, K. W. (1937). Experimental studies of learning and the higher mental processes in infrahuman primates. *Psychological Bulletin*, 34, 806-850.
- Tebbich, S., & Bshary, R. (2004). Cognitive abilities related to tool use in the woodpecker finch, *Cactospiza pallida*. *Animal Behaviour*, 67(4), 689-697.
- Tebbich, S., Taborsky, M., Fessler, B., & Blomqvist, D. (2001). Do woodpecker finches acquire tool-use by social learning? *Proceedings-of-the-Royal-Society-Biological-Sciences-Series-B*, 268(1482), 2189-2193.
- Thorndike, E. L. (1898). Animal intelligence: An experimental study of the associative processes in animals. *Psychological Monographs*, 2(4), 1-109.
- Thorpe, W. H. (1956). *Learning and instinct in animals.*: Harvard University Press.
- Thorpe, W. H. (1963). *Learning and Instinct in animals*. (2nd ed.). London: Methuen.
- Thouless, C. R., Fanshawe, J. H., & Bertram, B. C. R. (1989). Egyptian vultures *Neophron percnopterus* and Ostrich *Struthio camelus* eggs: the origins of stone-throwing behavior. *Ibis*, 131, 9-15.
- Timmermans, P. J. A., & Vossen, J. M. H. (2000). Prey catching in the archer fish: Does the fish use a learned correction for refraction? *Behavioural Processes*, 52(1), 21-34.
- Tomasello, M. (1996). Do apes ape? In C. M. Heyes & B. G. J. Galef (Eds.), *Social learning in animals: The roots of culture*. (pp. 319-346): Academic Press, Inc.
- Tomasello, M., & Call, J. (1997). *Primate cognition.*: Oxford University Press.

- Tomasello, M., Davis-Dasilva, M., Camak, L., & Bard, K. A. (1987). Observational learning of tool use by young chimpanzees. *Human Evolution*, 2(175 - 183).
- Visalberghi, E., & Tomasello, M. (1998). Primate causal understanding in the physical and psychological domains. *Behavioural Processes*, 42(2), 189-203.
- Weir, A. A. S. C., Jackie Kacelnik, Alex. (2002). Shaping of hooks in new caledonian crows. *Science*, 297(5583), 981.
- Whiten, A., & Ham, R. (1992). On the Nature and Evolution of Imitation in the Animal Kingdom: Reappraisal of a Century of Research. *Advances in the study of behavior.*, 21, 239 - 283.

Appendix A

This appendix provides a timeline for all major events in Loki's life. Entries referring to the introduction of new objects are indented.

	1998
Loki arrives	Jun 25
Experimenter begins using the word "Hello"	Jun 28
Loki begins caching (in small food/water bowls on perch)	Jul 4
Loki utters first two-syllable Eh-O vowel sounds	Jul 13
Loki begins to take food from fingers rather than swallowing	Jul 14
Loki begins to wean	Jul 18
Loki shows first evidence of cultural speciation	Jul 21
Drum and cymbal stands are installed in aviary	Jul 24
Activity center and associated objects in aviary	Jul 25
Experimenter finds food and objects (poker chips) in bath	Jul 31
First caches objects (poker chips) inside Cymbal box	Jul 31
Juvenile head moult in process	Aug 1
<u>Experiment 1</u>	
Baseline data are collected	Aug 3 - 9
Experimenter records and identifies several "Hello"s	Aug 3 - 9
Block I: Experimenter begins modeling	Aug 10
Drain cover found askew	Aug 5
Drain cover off completely	Aug 10
Drain cover off completely and one poker chip missing	Aug 17
Medium size rock placed on top of drain cover	Aug 20
Loki produces an "A" quality "Hello"	Sep 1
Block I: Modeling break	
Block II: Experimenter begins modeling	Nov 23
	1999
<u>OBS 1: Loki moves perch and accesses microphone</u>	Feb 3

Experimenter removes perch from aviary	Feb 4
Loki produces a "C" quality rendition of "Rap Rap"	Feb 9
Block II: Modeling break	Feb 23 – Mar 8
Continuation of observation for possible results from Exp 1	Mar 9 – Apr 25
Plastic water bottle installed	March
Plastic water bottle broken	March
Loki takes yellow lid from countertop	April 28
Plastic Square Crazy Link (orange)	May 6
Experimenter began tossing yellow lid	May 11
Experimenter began using word "catch"	May 22
Plastic Round Crazy Link (orange)	Jun 1
Frisbee	Jun 2
Plastic Practice Golf Ball (white)	Jun 5
Keychain	Jun 10
Loki takes Nozzle from countertop area	Jun 19
Plastic Spool (grey)	Jul 30
Light cycled to encourage molting	Aug 12 – 27
Loki is assessed by wildlife rehabilitator and determined to be a poor candidate for release	Aug 28 – Oct 16
Slinky (multicoloured)	Oct 16
Small Bell (silver)	Oct 19
Light cycled to encourage molting	Nov 1 – Dec 6
Hanging Shapes Parrot Toy on wall near perch	Nov 15
Food in Loki's food bowl is found to be wet	Dec
<hr/>	
	2000
Molt begins	Jan 27
CCTV camera & microphone installed on aviary ceiling	Jan 29
First videotape of Loki carrying Frisbee from bath to bowl	Feb 1
Food is found to be wet 20 minutes later	
Loki is observed carrying Frisbee repeatedly from bath to bowl, food can be seen on top of the Frisbee	Feb 1 – 15

Dry pan placed in room	Feb 12
Keychain, Bell, Nozzle removed from aviary	Feb 12
<u>OBS 2: Frisbee used for food and water portage</u>	Feb 17 – Mar 1
PVC Ring (white)	April 1
Nozzle returned to aviary	May 15
Food in bowl is not wet	May 20, 21, 22
Food and water puddles found on dry pan	Jun 20
Wiffle Ball (green)	July 18
Slinky is found hanging from perch (several wraps)	July 25
Small bowl is found inside large bowl (upside down)	July 26
Slinky is found hanging from perch (several wraps)	July 27, 28
Loki is seen pulling at floor end of hanging Slinky (CCTV)	Aug 4
First videotape (realtime) of Loki hanging Slinky	Aug 21
Spool (grey plastic) disappears (down drain)	Sep 30
Polymer Wine Cork (white)	Oct 3
Loki takes Hose Coupling (orange) from countertop	Oct 4
<u>OBS 3: Nozzle used for water portage</u>	Oct 30 – Nov 12
Loki uses Frisbee for object portage	
<u>Experiment 2</u>	
Baseline - Bath & Bowl	Oct 30 – Nov 12
Baseline - Pan	Nov 20 – Dec 3
Green Cup & Ring	Dec 4
Block 1	Dec 4 - 15
Block 2	Dec 16 - 27
Block 3	Dec 28 – Jan 8
	2001
Block 4 Missing Data	Jan 9 - 20
Block 5	Jan 21 – Feb 1

Block 6	Feb 2 — 13
Frisbee & Nozzle removed from aviary	Feb 5
Block 7	Feb 14 — 25
<u>OBS 4: Loki uses Slinky as headscratcher</u>	Feb 19
Block 8	Feb 26 — Mar 9
Block 9	Mar 10 - 21
Block 10	Mar 22 — Apr 2
Block 11	Apr 3 - 14
Block 12	Apr 15 - 26
Block 13	Apr 27 — May 8
Day 144 Bath: Cup dipped to side, acquired water	April 27
Day 146 Bowl: Cup with water placed, not poured, into bowl	April 29
Day 147 Dry Pan: Puddles are found, cup nearby	Apr 30
Day 149 Bowl: Food found awash with water	May 2
Block 14	May 9 - 20
Camera view changed to encompass both bath and bowl	May 21 — Jun 3

2002

Cup and Ring removed from aviary	Jan 24
Light cycled to encourage moulting	Oct 22 — Dec 14

2003

Loki moves to new room (1277A)	Mar 22
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Experiment 3

Baseline	Apr 28 — May 12
Frisbee, Green Cup, and Green Ring returned	May 12 — May 26

Experiment 4

Single Camera View of Bowl & Bath only

Baseline	Apr 28 - May 12
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Condition A	Bowl: Original	Tools: FR, GC, GR ²⁴	May 12 – May 26
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Single Camera View of Bowl Close-up only

Condition B	Bowl: Far	Tools: FR, GC, GR	May 26 – Jul 14
Condition C	Bowl: Far	Tools: GC, GR	Jul 14 – Jul 28
Condition D	Bowl: Original	Tools: GC, GR	Jul 28 – Aug 11
Condition A2	Bowl: Original	Tools: FR, GC, GR	Aug 11 – Aug 25

Two Camera Views: Bowl Close-up and Aviary Overhead View

Condition A3+Bowl:	Original	Tools: FR, GC, GR	Aug 25 – Sep 8
Condition B2+Bowl:	Far	Tools: FR, GC, GR	Sep 8 – Sep 22

²⁴ FR = Frisbee, GC = Green Cup, GR = Green Ring

Appendix B

Loki's Enrichment Items

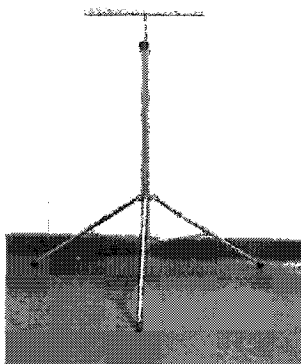


Figure B1. The lightweight tripod perch located in the aviary during Experiment 1 (note black rubber feet).

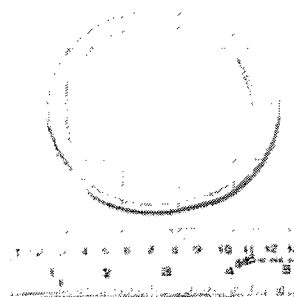


Figure B2. The yellow plastic lid used in the "catch" game.

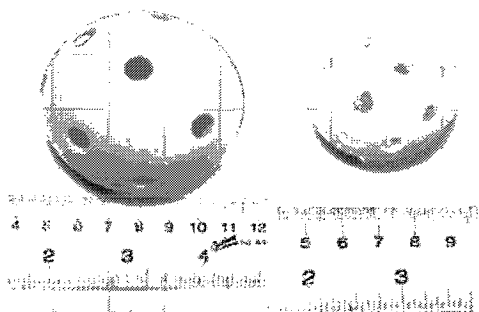


Figure B3. The two plastic balls used in the "toss" game.

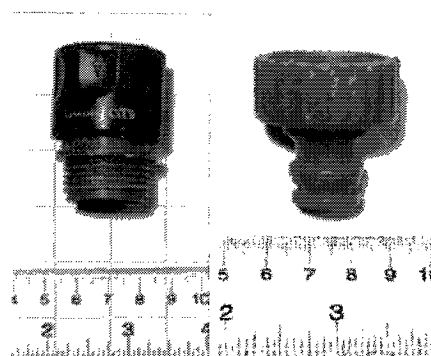


Figure B4. The green and orange plastic hose couplings.

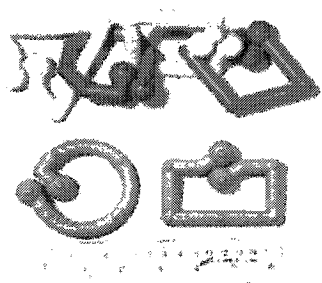


Figure B5. Plastic Crazy Links.

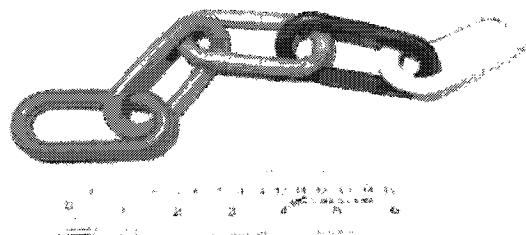


Figure B6. Plastic Link Chain.

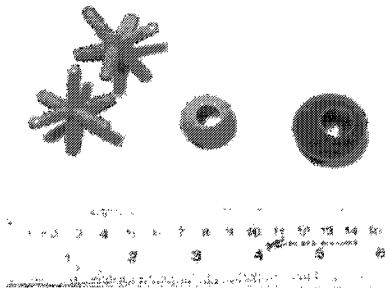


Figure B7. Assorted lightweight plastic jacks and heavier plastic beads.

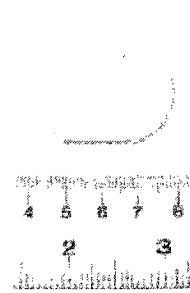


Figure B8. Plastic electrical outlet plug.

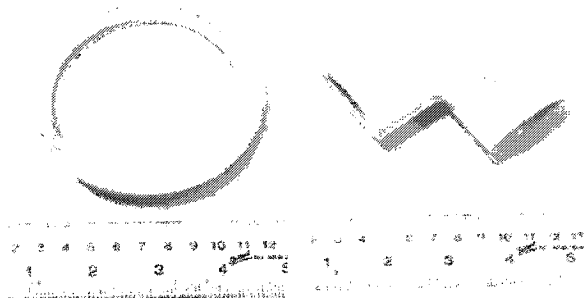


Figure B9. PVC ring and elbow.

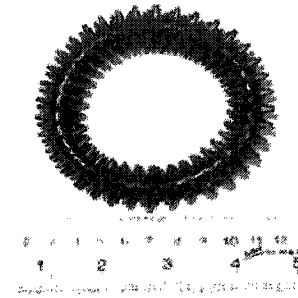


Figure B10. Purple canine teething ring.



Figure B11. Provides relative size comparisons of several of Loki's enrichment items, as well as showing two additional items: a toothbrush and two of the blue puckboard chips that were introduced in Experiment 1.

Appendix C

Description of Social+Object Games: *Catch* and *Toss*

Catch

In early May 1999, the Experimenter began tossing food bits (raisins or chow) to Loki across short distances. Crows are known to capture flying or jumping insects with precision (Kilham, 1989) and Loki was immediately adept at catching food bits when they were tossed to him. On May 11, 1999 Loki took, from the counter top, a bright yellow, soft plastic, coffee-can style lid which had previously capped a food container (See Appendix B, Figure B2). In attempting to recover it, a game of “catch” developed, where the Experimenter tossed the lid and Loki would catch it. This game started on the floor, with only a short distance between the two players, but quickly advanced to greater distances when Loki flew up to his perch (where he was usually stationed during food tosses) and oriented to the Experiment across the room. Tossing was fine for short distances, but of course, the Experimenter began to move further away thus making it necessary for the lid to be sailed horizontally, like a Frisbee, to cover the distance. On May 22, 1999 the Experimenter began using the words “Loki, Catch!” to indicate that a toss was imminent. Loki quickly learned to orient his body towards the Experimenter upon hearing these words and was a very good catcher.

After a successful catch the Experimenter approached Loki and placed outstretched hands under his beak in an attempt to retrieve the lid. If Loki was did not relinquish it, the Experiment grasped it with two fingers, at which time Loki would, almost always, simply let go. If he did not, the Experimenter walked away and went on about any remaining daily duties. However, Loki quickly began to surrender the item immediately by dropping it when requested. Catch was played most every day for at least a few throws. On one occasion, after Loki did not relinquish the Frisbee upon request, the Experimenter went and sat on the dog den. Loki dropped the Frisbee on the floor. The Experimenter remained seated. After a few moments, Loki flew down to the floor, picked up the lid, and

flew up and onto to the Experimenter's lap, with the lid in his beak. He dropped in the Experimenter's lab and then flew back to the perch. The Experimenter interpreted this as a solicitation to play and continued the game. Loki subsequently began approaching the Experimenter while holding other objects in his beak as well. In the case of the lid (the Experimenter's reactions to other objects are described below), the Experimenter took it and indicated a game of catch with the words "Loki, catch!" Loki would usually fly up to the perch and the game ensued. On June 2, 1999, the small dog Frisbee described in Chapter 3 (Figure 3.2) was introduced as a replacement for the plastic lid, which by now Loki had destroyed.

The Experimenter attempted to continue the catch game with the Frisbee. Unfortunately, it soon became apparent that it was an unsuitable substitute for the lid. For the Experimenter (who was never a serious contender), the Frisbee proved to be too heavy to sail accurately over short distances, and for Loki, it appeared to be uncomfortable to catch. After a few initial throws, he simply stopped cooperating by moving his head and/or entire body out of the Frisbee's trajectory. Nonetheless, he still seemed interested in the new object, so the Experimenter left the Frisbee in the corner near the den upon exiting the aviary. This is the same Frisbee that later served as Loki's first portage tool.

The yellow lid was never again included as an item in Loki's toy collection once the Frisbee arrived. Nonetheless, in between experiments, catch is still instigated by the Experimenter two or three times a month with another yellow lid rather than the Frisbee, and Loki is still an excellent catch partner.

Toss

As stated earlier, Loki began to approach the Experimenter with objects other than the lid. Most were ignored. However, when Loki approached the Experimenter with a ball (Appendix B, Figure B3), *toss* began. The Experimenter took the ball from Loki's beak, or picked it up if he had dropped it directly, and then rolled it across the aviary floor. Loki often retrieved the ball by picking it up in his beak, and then lifting his head, he would release/toss the ball in the general

direction of the Experimenter. When this happened, the Experimenter would retrieve the ball and once again roll it across the floor. This continued until Loki no longer retrieved the ball.

Over the last two years Loki has approached the Experimenter less often for a game of toss. He has developed an alternative behavior. When alone, he often rolls or tosses the ball, and other items, onto or around in the dry pan. The raised pan-edge keeps the objects from rolling out, and the different objects make a wide range of clanging sounds as they come in contact with the stainless steel (see DV 13-18). The Experimenter played catch and toss games only during aviary cleaning/socialization time.

Appendix D

Supplementary Digital Video^s

Eighteen supplementary digital videos, described below, can be found on the enclosed CD-ROM.

File Name	Format	Description
DV1	.mpg	Tool Use A sound-activated video showing the mobile perch moving across the aviary floor until positioned underneath the microphone. After which, Loki boards the perch and begins a sustained bout of pecking at the microphone.
DV2	.mpg	Tool Use Three views of Loki using a small Frisbee to acquire and then deliver water to his food bowl. The first two views were recorded in real-time, the last one is time-lapse slowed to near real-time.
DV3	.mpg	Tool Use Three views of Loki using a small Frisbee to acquire and then deliver food to the water pan. The first view was recorded in real-time, the last two are time-lapse, slowed to near real-time.
DV4	.mpg	Tool Use A time-lapse video, slowed to near real-time, showing Loki using a small Frisbee to scoop up and carry

away food from the bowl after the removal of a problematic object.

DV5	.mpg	<p>Tool Use</p> <p>A composite video sequence that first shows Loki flying with the Slinky and securing it to the perch (real-time), then shows Loki on the floor (time-lapse slowed to near real-time), grasping the Slinky, pulling it back and letting it go, thereby setting it in motion, after which he moves under the swinging Slinky until it makes contact with his head and neck and provides a head scratch. The results of three additional grasp/pull/approaches are also shown.</p>
DV6	.mpg	<p>Tool Use</p> <p>Time-lapse video, slowed to near real-time, showing Loki approaching the bath with the cup in his beak; the keychain is inside. Once deposited, the cup is tipped over somewhat by the weight of the item inside. With a beak-push the cup's edge submerges and fills, and water (arrow) can be seen spilling from it as it is carried away.</p>
DV7	.mpg	<p>Tool Use</p> <p>Time-lapse video, slowed to near-real-time, showing Loki approaching the bath with the cup in his beak, the orange plastic hose coupling is inside. Once deposited, the cup is tipped over somewhat by the weight of the item inside. With a beak-push the cup's edge submerges and fills, and water (arrow) can be seen spilling from it as it is carried away.</p>

DV8	.mpg	<p>Tool Use</p> <p>Time-lapse video, slowed to near real-time, showing Loki approaching the bath with the cup in his beak. Note the green toy object inside the cup. Once deposited, the cup fell onto its side as a result of the relatively heavy item it contained. In this particular instance, when Loki retrieved the water-filled cup and carried it away, the toy remained in the bath.</p>
DV9	.mpg	<p>Tool Use</p> <p>Time-lapse video, slowed to near real-time, showing Loki placing a water-filled cup into his food bowl and then pouring out the contents.</p>
DV10	.mpg	<p>Play</p> <p>Real-time video showing Loki hanging the Slinky on the perch and then engaging in a sustained bout of play directed towards the free end.</p>
DV 11	.mpg	<p>Play</p> <p>A real-time video showing Loki repeatedly rolling the Frisbee on top of a stainless steel "skewer".</p>
DV12	.mpg	<p>Play</p> <p>Time-lapse video showing Loki tossing the Frisbee and the PVC ring around on the dry pan, and then setting the PVC ring up on its edge and skillfully rolling it against the edge of the pan, and around the nearby floor area.</p>

DV13	.mpg	Play A time-lapse video showing Loki rolling the green plastic ball around on the dry pan.
DV14	.mpg	Play A time-lapse video showing Loki tossing the keychain around on the dry pan, and then flying away with it.
DV15	.mpg	Play A time-lapse video showing Loki tossing, from a distance, the white plastic ball onto the dry pan.
DV16	.mpg	Play A time-lapse video showing Loki tossing the orange hose coupling onto the dry pan from the perch.
DV17	.mpg	Play A time-lapse video showing Loki tossing the orange hose coupling onto the dry pan from the perch.
DV18	.mpg	Play A time-lapse video showing Loki tossing the orange hose coupling onto the dry pan from the floor.

[§] These digital video files have been provided as supplementary material for the dissertation entitled *The Ontogenesis of Innovative Tool Use in an American Crow (Corvus brachyrhynchos)*, by Patricia D. Cole, submitted in partial fulfillment for the degree of Doctor of Philosophy to Dalhousie University, Halifax, Nova Scotia, Canada, August 2004. **These videos are the copyrighted property of Patricia D. Cole and may not be distributed without her written permission.**