



On the evolutionary and ontogenetic origins of tool-oriented behaviour in New Caledonian crows (*Corvus moneduloides*)

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New Caledonian crows (*Corvus moneduloides*) are prolific tool users in captivity and in the wild, and have an inherited predisposition to express tool-oriented behaviours. To further understand the evolution and development of tool use, we compared the development of object manipulation in New Caledonian crows and common ravens (*Corvus corax*), which do not routinely use tools. We found striking qualitative similarities in the ontogeny of tool-oriented behaviour in New Caledonian crows and food-caching behaviour in ravens. Given that the common ancestor of New Caledonian crows and ravens was almost certainly a caching species, we therefore propose that the basic action patterns for tool use in New Caledonian crows may have their evolutionary origins in caching behaviour. Noncombinatorial object manipulations had similar frequencies in the two species. However, frequencies of object combinations that are precursors to functional behaviour increased in New Caledonian crows and decreased in ravens throughout the study period, ending 6 weeks post-fledging. These quantitative observations are consistent with the hypothesis that New Caledonian crows develop tool-oriented behaviour because of an increased motivation to perform object combinations that facilitate the necessary learning. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **102**, 870–877.

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INTRODUCTION

New Caledonian crows (*Corvus moneduloides*; hereafter NC crows) are among the most prolific and sophisticated nonhuman tool users (Hunt & Gray, 2006; Bluff *et al.*, 2007). The species has an inherited predisposition for tool-oriented behaviours (TOB) (Kenward *et al.*, 2005; Kenward *et al.*, 2006; Hunt, Lambert & Gray, 2007), although there is also evidence of individual creativity in tool manufacture and tool-related problem-solving (Weir, Chappell & Kacelnik, 2002; Taylor *et al.*, 2010; Weir & Kacelnik,

2006; Wimpenny *et al.*, 2009), as well as the possibility that tool patterns are culturally transmitted in the wild (Bluff, Kacelnik & Rutz, 2010a; Bluff *et al.*, 2010b; Holzhaider, Hunt & Gray, 2010a; Hunt & Gray, 2003). This constellation of traits raises questions regarding the evolutionary and ontogenetic origins of TOB, as well as the putative relation between TOB and general intelligence. In the present study, we present a comparison of the development of object-oriented behaviours, of which TOB is a subset, in NC crows and common ravens (*Corvus corax*), comprising a related species to which similar cognitive abilities are attributed (Bugnyar & Heinrich, 2005; Heinrich & Bugnyar, 2005) but that does not regularly use tools in the wild.

Behavioural traits, just like structural features, can evolve for a specific function and then be co-opted to serve new purposes (Baerends, 1975). Avian courtship behaviour, for example, has been suggested to have originated from a range of different behaviours,

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including coition, preening, agonistic displays, and juvenile begging (Huxley, 1923; Tinbergen, 1952). We have reported previously that functional TOB in NC crows develops through an interplay between learning and maturation of a suite of inherited stereotyped action patterns (Kenward *et al.*, 2006). If some of these action patterns turn out to be shared with ravens, this would suggest that they are the legacy of a common, nontool-using ancestor. Such comparisons, which comprise the first objective of the present study, can inform speculation about the possible evolutionary origins of TOB in NC crows. We note, however, that this approach is not suitable for investigating why tool use has been selected for only in NC crows; this is a question on a different explanatory level (Tinbergen, 1963) and one that is not addressed here.

Evolutionary precursors have been proposed for a range of tool using behaviours (Alcock, 1972): Egyptian vultures (*Neophron percnopterus*), which break large eggs by throwing stones at them, also break smaller eggs by throwing the eggs themselves, using similar movements (Alcock, 1970; Thouless, Fanshawe & Bertram, 1989); ant-lions (*Myrmelon* spp.) knock prey into the bottom of a pit trap by propelling sand at them using the same head-tossing movements as they use to construct and maintain the pit; and archer fish (*Toxotes jaculatrix*), which shoot jets of water at insects to knock them down, do so by closing their gill covers, an action that they also perform before leaping out of the water to pursue insects close to the surface. In NC crows themselves, foraging in leaves of *Pandanus* spp. trees by ripping at the base has been suggested as a potential precursor for *Pandanus* leaf-tool manufacture (Hunt & Gray, 2003).

One candidate for an evolutionary precursor for TOB in NC crows is food-caching, which is performed to some degree by almost all corvid species, including NC crows (Hunt, 2000; Kenward *et al.*, 2006), and the inferred common ancestor (de Kort & Clayton, 2006). Structurally, caching and TOB both involve the insertion of objects into substrates. Furthermore, the privileged knowledge of caching animals about the presence of out-of-sight food in cavities may foster a special interest in exploring cavities and create the opportunity for the modification of motor patterns that evolved for caching. If the developmental pathway that originally led to caching in ancestral NC crows was evolutionarily co-opted for tool use, we would expect to see qualitative similarities in the behaviours displayed during the ontogeny of caching in ravens and tool use in NC crows. Three other possible precursor behaviours are: (i) nest building (Alcock, 1972; Hansell & Ruxton, 2008), which involves handling and manipulating twigs; (ii) killing live prey, which, in corvids, involves rubbing and

jabbing movements similar to some developmental precursor TOB behaviours (J. Marzluff, pers. comm.); and (iii) *Pandanus* leaf ripping, which might have led to tool use if leaf fragments were retained in the beak when foraging at *Pandanus* leaf bases (as suggested by an anonymous referee).

The second objective of our developmental comparison is to shed further light on the ontogenetic mechanisms by which, among the corvids, only NC crows normally develop tool use in the wild. We have asserted that NC crow TOB is a specifically evolved trait (Kenward *et al.*, 2005; Kenward *et al.*, 2006) but the fact that rooks (*Corvus frugilegus*) can perform a variety of tool use and manufacture techniques in the laboratory indicates that corvid species may not differ greatly with respect to the cognitive abilities that facilitate tool use (Bird & Emery, 2009). To reconcile the latter view with the observation that only NC crows normally express TOB in the wild, it has been suggested that NC crows may have evolved to differ primarily in their motivation to use tools, rather than in general cognitive capacity (Kacelnik, 2009). Object combination is a necessary part of tool use. If juvenile NC crows combine objects more often than ravens, in a 'play-like' fashion before objects are used as tools, this could therefore be interpreted as supporting the existence of a motivational bias in NC crows, independent of the degree of general problem-solving ability.

MATERIAL AND METHODS

We examined original data on the development of object-oriented behaviour in ravens and re-analyzed data from previously published studies on NC crow ontogeny (Kenward *et al.*, 2005; Kenward *et al.*, 2006). Four NC crows (three male, one female) and twelve ravens (six males, six females) were hand-raised in artificial nests and then housed in free-flying aviaries enriched with twigs and toys, with many holes and crevices in various substrates, and with *ad libitum* access to food and water. The birds were regularly observed by an observer present in the aviary, using a focal-individual approach. We analyzed data from one week pre-fledging to six weeks post-fledging.

It is impossible to compare behavioural development across species with full control of the environment because the marked spontaneous differences in behaviour necessarily induce early environmental differences. Furthermore, neither of the study species is easily reared in captivity in the controlled fashion that is feasible with the short-generation-time model species typically used in developmental research. In addition to unavoidable differences, although the housing and observation conditions for the two

species were similar, there were differences as a result of the post-hoc nature of the study comparisons: crows lived in pairs (one pair was separated three weeks post-fledging), ravens in one large group; crows hatched in captivity, ravens were taken from natural nests pre-fledging; observation session durations and frequencies were 30 min, 1.8 times per day per individual for crows, and 5 min, 0.6 times per day per individual for ravens; crows were observed individually, ravens when in their social group. Most importantly, two crows (referred to as the ‘tutored’ crows) were regularly exposed to human demonstration of twig tool use (as part of a study into social influence of the acquisition of TOB; Kenward *et al.*, 2006), and two crows (‘untutored’) never saw tool use, although they did receive the same level of contact with the human foster parent. There were significant quantitative (though not qualitative) effects of tutoring on some parameters of tool use development. For these variables (identified later), we therefore present data from the tutored and untutored NC crows separately.

We define ‘manipulation’ as any behaviour in which the beak or foot holds an object, and ‘combination’ as any manipulation in which an object is placed in contact with another object or substrate. We divide combination into two categories: ‘precursors’, which we define as combinations which are not immediately functional, and ‘functional insertion’, a behaviour required for caching and/or tool use, in which an item is placed inside a hole or crevice. Precursor behaviours for ravens (Clayton, 1992; Bugnyar, Stöwe & Heinrich, 2007b) and NC crows (Kenward *et al.*, 2006) have been defined previously. In ravens, precursor combination takes the form of ‘placement’, in which objects are pressed against a substrate. The most common precursor combination in NC crows is ‘rubbing’, in which objects are rubbed against substrates such as perches, using actions similar to those that adults use functionally to probe crevices. Other NC crow precursor combinations are variants of rubbing specifically performed with twigs. For example, ‘proto-probing’ involves holding a twig in a manner appropriate for probing a hole or crevice, touching it against a substrate that is not a hole or crevice (e.g. the side of a perch), and moving it back-and-forth against the substrate, whereas ‘poking’ involves holding a twig and jabbing the end against any flat substrate.

To test for quantitative species differences in behaviour frequency, using MINITAB 14 (Minitab Inc.), we fitted general linear mixed models (GLMMs), with sequential sums of squares, entering the predictor variables in the order: ‘age since fledging’ (covariate), ‘species’ (fixed factor), ‘individual bird’ (random factor nested in ‘species’ – the inclusion of this term allows

the valid analysis of repeated measures on individuals, Kutner *et al.*, 2004), the ‘age × species’ interaction, and the ‘age × individual’ interaction. Where necessary, we also fitted models separately for the two species. Dependent variables that were proportions were arcsine square-root transformed to normalize errors, and rate variables were square-root transformed. We checked model fits by inspecting diagnostic scatter plots, using standardized residuals (Grafen & Hails, 2002).

Testing ravens but not crows in a social group might have led to biased measures of between-species differences in object manipulation. To rule out any effects of direct influence by conspecifics at time of testing, we therefore repeated all analyses excluding all manipulations initiated by nonfocal individuals. This did not affect any of our conclusions, and we therefore present the results obtained with the full datasets. We discuss later the possible longer-term effects of raising in different group sizes.

RESULTS

QUALITATIVE COMPARISON OF DEVELOPMENTAL STEPS: FUNCTIONAL BEHAVIOURS AND THEIR PRECURSORS

In both species, development of functional caching or tool use was preceded by precursor combinations (Fig. 1). In both species, in precursor and functional combinations, the object in question was sometimes left against the substrate and sometimes retained in the beak, although typically left in ravens and retained in NC crows (because this was not formally recorded for ravens, quantitative analyses of this difference were impossible). NC crows often accompanied insertion with rhythmical back-and-forth movements of the object being held (Kenward *et al.*, 2006). Ravens usually accompanied insertion with repeated touching and/or slightly re-positioning of the cached object (Bugnyar *et al.*, 2007b). Later in development (primarily outside the time frame of this comparison), ravens began covering inserted items by other objects, as seen in fully-developed raven caching. In both species, combination therefore began by placing objects against a substrate, and progressed to placing objects inside substrate concavities and manipulating the object inside the crevice or cache.

QUANTITATIVE COMPARISON OF OBJECT MANIPULATION AND COMBINATION

The two species did not differ significantly in the amount of time they spent manipulating all object types combined ($F_{1,12.5} = 0.08$, $P = 0.780$; Fig. 2A). The mean ($\pm 95\%$ confidence interval) percentage of observed time spent manipulating all objects were

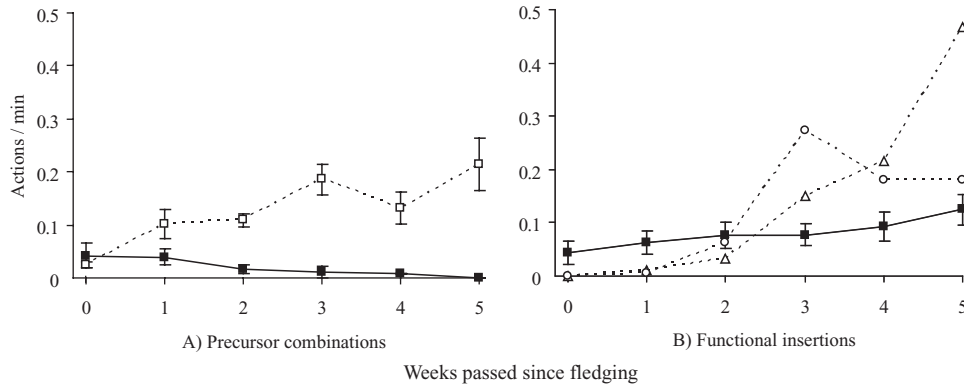


Figure 1. The development of (A) precursor combinations (e.g. rubbing, placement) and (B) functional insertion in four New Caledonian (NC) crows (---□---) and twelve Common ravens (—■—) (weekly mean ± SE). Data are shown separately in (B) for two untutored (---○---) and two tutored NC crows (---△---) because the groups differed in functional insertion (Kenward *et al.*, 2006) and error bars are omitted because $N = 2$. Fledging occurred at the beginning of week 0.

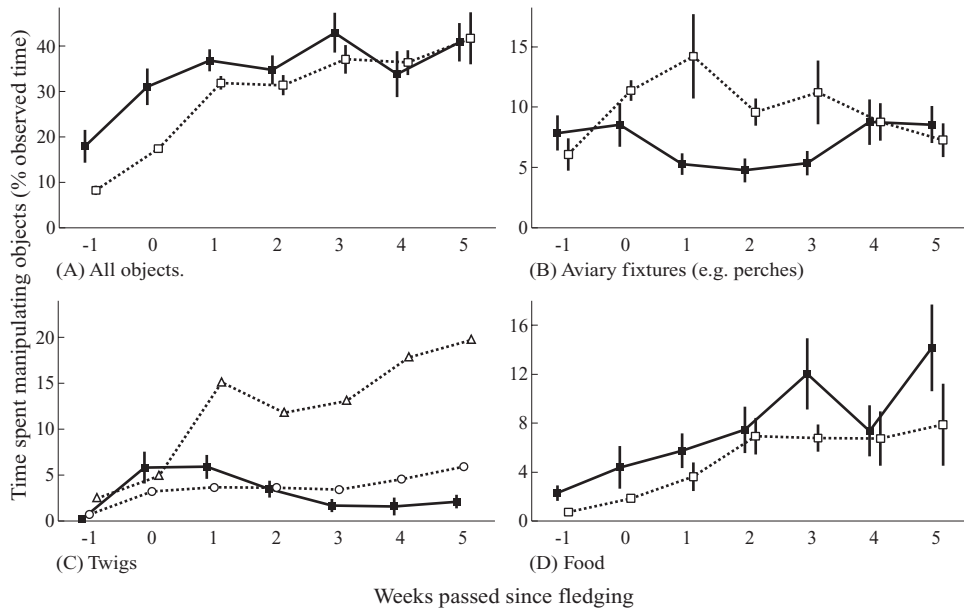


Figure 2. Proportion of time spent manipulating objects by four New Caledonian (NC) crows (---□---) and twelve Common ravens (—■—) (weekly mean ± SE). Data are shown separately in (C) for two untutored (---○---) and two tutored NC crows (---△---) because the groups differed in twig manipulation (Kenward *et al.*, 2006) and error bars are omitted because $N = 2$. Note that the variables shown in different panels are non-independent as a result of the unit-sum constraint inherent in proportional data. Fledging occurred at the beginning of week 0.

30 ± 8% for NC crows and 34 ± 4% for ravens, indicating that it is unlikely that there is a considerable but undetected species difference in frequency, and even more unlikely that such putative difference would favour the tool-using NC crows. Manipulation of all objects increased significantly with age in both NC crows ($F_{1,7.1} = 94.63$, $P < 0.001$) and ravens ($F_{1,362.0} = 20.97$, $P < 0.001$), although the rate of increase was significantly higher in NC crows than in ravens (significant ‘age × species’ interaction term;

$F_{1,633.0} = 5.68$, $P = 0.011$). It was possible for the NC crows to have a higher rate of increase without a higher overall level because they began the period with a lower level (Fig. 2A). NC crows spent significantly more time manipulating aviary fixtures than ravens ($F_{1,11.2} = 22.68$, $P = 0.001$); this effect was mainly attributable to the first weeks post-fledging (Fig. 2B).

Visual inspection of the figures suggests that tutored NC crows manipulated twigs considerably

more often than either their untutored counterparts or ravens, whereas untutored NC crows did not differ much from ravens (Fig. 2C; small sample sizes for separated NC crow groups preclude statistical modelling). We found no strong species difference with respect to food manipulation (Fig. 2D; a GLMM with the best possible transformations showed a significant effect only of age but had poor fit according to diagnostic plots).

The quantitative analysis of combinatorial behaviours reveals that precursor combination frequencies differed substantially between the species (Fig. 1A): NC crows performed more precursor combinations ($F_{1,15.5} = 75.4$, $P < 0.001$). As confirmed by a significant 'age \times species' interaction term ($F_{1,61.0} = 19.33$, $P < 0.001$), NC crows increased their precursor rate over the whole observation period ($F_{1,13.9} = 15.91$, $P = 0.001$), whereas ravens decreased their rate ($F_{1,48.0} = 11.83$, $P = 0.001$). Small sample sizes for separated NC crow groups precluded statistical modelling of functional combination frequency, although trends can be seen in Figure 1B. Note that in the crows, although tuition was found to increase the rate of functional twig insertion, tuition was not found to affect precursor behaviours (Kenward *et al.*, 2006), and precursor rates are much higher in all crows than in ravens.

Seven of the twelve ravens performed combinations with twigs, at a mean \pm SE rate (pooled over the study period) of 0.77 ± 0.30 combinations per hour; 38% of these events were insertions. All four NC crows performed combinations with twigs, with untutored NC crows performing 1.49 ± 0.11 combinations with twigs per hour (of which 17% were insertions), and tutored NC crows performing 8.50 ± 1.93 combinations per hour (of which 37% were insertions). Small sample sizes for separated NC crow groups precluded statistical modelling.

DISCUSSION

THE EVOLUTION OF NEW CALEDONIAN CROW TOOL-ORIENTED BEHAVIOUR

The development of object-oriented behaviour was qualitatively very similar in both species. The precursor behaviours in NC crows are structurally similar to placement in ravens, in that both behaviours involve positioning small objects on substrates, and both species' early behaviours develop into inserting, which is similar between the species not only in that objects are put inside cavities, but also in that they are usually repeatedly repositioned. The differences that do exist (e.g. NC crows' higher probability of retaining the object, and their more rhythmical post-insertion movements) may be seen as variations of

this common template. Under the reasonable assumption that traits that are shared by closely-related species are more likely to be derived from a common ancestor, rather than having evolved independently, these observations support the hypothesis that caching and TOB develop from the same precursor behaviours and therefore that the inherited action patterns for TOB not shared with ravens may have evolved from movements related to caching. This hypothesis is further supported by the observation that most of the ravens cached twigs (Heinrich & Smolker, 1998), as well as the fact that wild ravens handle twigs in non-nest-related contexts and cache nonfood objects (T. Bugnyar, pers. observ.; see also Bugnyar *et al.*, 2007a). Other corvids are also known to handle and cache nonfood items: captive juvenile and adult rooks manipulate sticks (Seed *et al.*, 2006; Tebbich *et al.*, 2007; Bird & Emery, 2009) and captive adult Eurasian jays (*Garrulus glandarius*) cache stones (Clayton, Griffiths & Bennett, 1994).

It is important to note that the common ancestor of ravens and NC crows was almost certainly a caching species (de Kort & Clayton, 2006). Given that the most recent nontool-using ancestor of NC crows almost certainly cached, it is likely that it also would occasionally have cached twigs during the development of object-oriented behaviour. Indeed, during the early stages of development, the study ravens inserted objects and withdrew them without letting go, which is an element of twig tool use as observed in NC crows. In the tropical environment of New Caledonia (i.e. rich in insect prey available under tree bark), this would have provided opportunities to accidentally obtain food. Under this scenario, the action patterns already possessed by the ancestral caching species could have been modified by natural selection into TOB.

We are not predicating that caching is a universal precursor of tool use across species. The woodpecker finch (*Cactospiza pallida*), which also has an inherited predisposition to use twig tools (Tebich *et al.*, 2001), does not cache, and neither do its closest relatives. However, different developmental precursor TOB behaviours are seen in woodpecker finches and NC crows (S. Tebbich, pers. comm.), suggesting different evolutionary origins. Other possible phylogenetic precursors for TOB are the actions involved in nest building (Alcock, 1972; Hansell & Ruxton, 2008), killing live prey (J. Marzluff, pers. comm.), and foraging in *Pandanus* leaves by ripping. The data reported in the present study do not rule out these various possibilities, which in any case are not necessarily mutually exclusive. Food-caching, however, shares all six traits with TOB: (i) it entails inserting objects into small cavities, with subsequent repositioning; (ii) it involves twig insertion as an early

developmental precursor; (iii) it predominantly involves food; (iv) it provides the animal with privileged knowledge about the presence of out-of-sight food; (v) it has a developmental pattern strikingly similar to TOB; and (vi) it is a less common behaviour than alternative evolutionary precursors, so better accounts for the rarity of avian tool use. Nest building shares only the first two traits; prey killing only the third and sixth; and *Pandanus* ripping only the third, fourth, and sixth. For this reason, food-caching is currently the most parsimonious candidate for the evolutionary precursor of NC crow TOB. We acknowledge, however, that an argument based on such reasoning cannot be conclusive, and that this study should therefore be seen predominantly as a starting point for further research. We further note that none of these hypotheses for the evolutionary origins of the first NC crow TOB can account for the more complex forms of TOB such as hook manufacture, which presumably evolved subsequently to simple tool use.

THE ONTOGENY OF NEW CALEDONIAN CROW TOOL-ORIENTED BEHAVIOUR

We now examine what the quantitative data obtained in the present study can contribute to the question of what is special about NC crow ontogeny that causes them (uniquely among the corvids) to develop widespread tool use. We note that, although we assert that NC crows inherit action patterns specialized for tool use (Kenward *et al.*, 2006), heritable action patterns do not provide a complete explanation, for three reasons. First, as we have demonstrated in the present study, other corvid species inherit very similar action patterns. Second, other corvid species can learn to use tools without it being an inherited specialization (Boswall, 1983; Bird & Emery, 2009). Third, there is a substantial learning component in the ontogeny of NC crow TOB (Kenward *et al.*, 2006; Holzhaider, Hunt & Gray, 2010b).

The two study species did not display major observable differences in their tendencies to perform non-combinatorial object manipulations with all objects, and untutored crows did not display major observable differences to ravens in their tendency to perform noncombinatorial manipulations on twigs. These observations indicate two points. First, the quantitative species differences observed in combinatorial behaviour are unlikely to result solely from differences in the respective physical rearing environments; if, for example, small objects had been more salient in the NC crows' environment, one would have observed not only more combinations involving small objects, but also more overall manipulation of them. Second, as claimed previously (Kenward *et al.*, 2006), acquisition of TOB in NC crows is unlikely to be the

result of a general manipulatory tendency coupled with learning; it appears that something more specific, related to combination, is inherited.

It has been suggested that the key difference in NC crow psychology may be a motivation to perform actions associated with tool use (Kacelnik, 2009). The results concerning precursor combination are consistent with this view; although, in ravens, precursor object combination had been almost entirely replaced by functional caching behaviour by the end of the study period, in NC crows, precursor combination rates were still high and continued to increase throughout the study. In the two NC crows that did not receive tutoring (which increased functional combination, Kenward *et al.*, 2006), functional combination was still at a lower level than precursor combination by the end of the study period, despite the fact that all crows were capable of successful tool-mediated food retrieval by that point. It should be noted that precursor combinations in NC crows, despite an adherence to the general template of combining an object with a substrate followed by rubbing or poking movements, are somewhat variable in finer details (Kenward *et al.*, 2006). We therefore suggest that the increased motivation possessed by NC crows compared to other corvids may not be to perform specific tool-oriented behaviours but rather to persist in performing somewhat plastic object combinations (Bluff *et al.*, 2010b), which with time facilitates learning of the wide variety of tool use techniques found in the wild (Hunt & Gray, 2006; Holzhaider *et al.*, 2010b). In other words, we suggest that NC crows are more inclined to object-combination play (Burghardt, 2005). This account is consistent with those of how primate species acquire tool use (Fragaszy & Adams-Curtis, 1991; Lockman, 2000).

An alternative explanation for the species difference in precursor object combination rates also requires attention. It is possible that the larger group size in ravens led to a relative reduction in precursor combinations (e.g. because of increased interference). We do not favour the hypothesis that such social influences are important for NC crow and raven precursor combination rates because it makes a number of other predictions that have not been borne out. First, in a previously observed group of fledgling ravens half the size (six rather than twelve ravens) and kept at a 40% lower density (33 rather than 20 m² per raven) in a very similar physical environment (Bugnyar *et al.*, 2007b), the precursor combination rate was almost identical to that reported in the present study, with a trend for more precursor combination in the larger group (group means were 1.08 and 1.20 combinations per hour, respectively, over the period reported in the present study, compared to 7.68 for NC crows). Second, it is likely that such a group

size effect would influence not only precursor object combination but also overall object manipulation, although there was no species difference observed in overall object manipulation. Third, if precursor manipulation was sensitive to social influence, tutoring would be likely to affect it in NC crows, although there was no such effect observed (Kenward *et al.*, 2006). We note finally that group size differences in the same direction as that present in our comparison are present in wild populations: juvenile NC crows are found predominantly in small family groups through their first year (Kenward *et al.*, 2004; Holzhaider *et al.*, 2010b, c), whereas juvenile ravens begin integrating into large flocks by the end of our study period (Boarman & Heinrich, 1999; T. Bugnyar, pers. observ.). Keeping group size constant across species would therefore have raised questions about the ecological validity of our comparison.

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REFERENCES

- Alcock J. 1970.** The origin of tool-using in Egyptian vultures (*Neophron percnopterus*). *Ibis* **112**: 542–542.
- Alcock J. 1972.** The evolution of the use of tools by feeding animals. *Evolution* **26**: 464–473.
- Baerends GP. 1975.** An evaluation of the conflict hypothesis as an explanatory principle for the evolution of displays. In: Baerends G, Beer C, Manning A, eds. *Function and evolution in behaviour*. Oxford: Clarendon Press, 187–227.
- Bird CD, Emery NJ. 2009.** Insightful problem solving and creative tool modification by captive nontool-using rooks. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 10370–10375.
- Bluff LA, Weir AAS, Rutz C, Wimpenny JH, Kacelnik A. 2007.** Tool-related cognition in New Caledonian crows. *Comparative Cognition and Behavior Reviews* **2**: 1–25.
- Bluff LA, Kacelnik A, Rutz C. 2010a.** Vocal culture in New Caledonian crows *Corvus moneduloides*. *Biological Journal of the Linnean Society* **101**: 767–776.
- Bluff LA, Troscianko J, Weir AAS, Kacelnik A, Rutz C. 2010b.** Tool use by wild New Caledonian crows *Corvus moneduloides* at natural foraging sites. *Proceedings of the Royal Society of London Series B, Biological Sciences* **277**: 1377–1385.
- Boarman WI, Heinrich B. 1999.** Common raven (*Corvus corax*). In: Poole A, Gill F, eds. *Birds of North America*, No. 476. Philadelphia, PA: The Birds of North America, Inc.
- Boswall J. 1983.** Tool-using and related behaviour by birds: yet more notes. *Avicultural Magazine* **89**: 170–181.
- Bugnyar T, Heinrich B. 2005.** Ravens, *Corvus corax*, differentiate between knowledgeable and ignorant competitors. *Proceedings of the Royal Society of London Series B, Biological Sciences* **272**: 1641–1646.
- Bugnyar T, Schwab C, Schloegl C, Kotrschal K, Heinrich B. 2007a.** Ravens judge competitors through experience with play caching. *Current Biology* **17**: 1804–1808.
- Bugnyar T, Stöwe M, Heinrich B. 2007b.** The ontogeny of caching in ravens, *Corvus corax*. *Animal Behaviour* **74**: 757–767.
- Burghardt GM. 2005.** *The genesis of animal play: testing the limits*. Cambridge, MA: MIT Press.
- Clayton NS. 1992.** The ontogeny of food-storing and retrieval in marsh tits. *Behaviour* **122**: 11–25.
- Clayton NS, Griffiths D, Bennett ATD. 1994.** Storage of stones by jays (*Garrulus glandarius*). *Ibis* **136**: 331–334.
- de Kort SR, Clayton NS. 2006.** An evolutionary perspective on caching by corvids. *Proceedings of the Royal Society of London Series B, Biological Sciences* **273**: 417–423.
- Fragaszy DM, Adams-Curtis LE. 1991.** Generative aspects of manipulation in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology* **105**: 387–397.
- Grafen A, Hails R. 2002.** *Modern statistics for the life sciences*. Oxford: Oxford University Press.
- Hansell M, Ruxton GD. 2008.** Setting tool use within the context of animal construction behaviour. *Trends in Ecology and Evolution* **23**: 73–78.
- Heinrich B, Bugnyar T. 2005.** Testing problem solving in ravens: string-pulling to reach food. *Ethology* **111**: 962–976.
- Heinrich B, Smolker R. 1998.** Play in common ravens (*Corvus corax*). In: Bekoff M, Byers JA, eds. *Animal play: evolutionary, comparative, and ecological perspectives*. Cambridge: Cambridge University Press, 27–44.
- Holzhaider JC, Hunt GR, Gray RD. 2010a.** The development of pandanus tool manufacture in wild New Caledonian crows. *Behaviour* **147**: 553–586.
- Holzhaider JC, Hunt GR, Gray RD. 2010b.** Social learning in New Caledonian crows. *Learning & Behavior* **38**: 206–219.
- Holzhaider JC, Sibley MD, Taylor AH, Singh PJ, Gray RD, Hunt GR. 2010c.** The social structure of New Caledonian crows. *Animal Behaviour*. Advance online publication. doi:10.1016/j.anbehav.2010.09.015
- Hunt GR. 2000.** Tool use by the New Caledonian crow *Corvus moneduloides* to obtain Cerambycidae from dead wood. *Emu* **100**: 109–114.
- Hunt GR, Gray RD. 2003.** Diversification and cumulative evolution in New Caledonian crow tool manufacture.

- Proceedings of the Royal Society of London Series B, Biological Sciences* **270**: 867–874.
- Hunt GR, Gray RD. 2006.** Tool manufacture by New Caledonian crows: chipping away at human uniqueness. *Acta Zoologica Sinica* **52** (Suppl.): 622–625.
- Hunt GR, Lambert C, Gray RD. 2007.** Cognitive requirements for tool use by New Caledonian crows (*Corvus moneduloides*). *New Zealand Journal of Zoology* **34**: 1–7.
- Huxley JS. 1923.** Courtship activities in the red throated diver (*Colymbus stellatus* Pontopp.); together with a discussion of the evolution of courtship in birds. *Journal of the Linnean Society (Zoology)* **35**: 253–292.
- Kacelnik A. 2009.** Tools for thought or thoughts for tools? *Proceedings of the National Academy of Sciences of the United States of America* **106**: 10071–10072.
- Kenward B, Rutz C, Weir AAS, Chappell J, Kacelnik A. 2004.** Morphology and sexual dimorphism of the New Caledonian crow *Corvus moneduloides*, with notes on its behaviour and ecology. *Ibis* **146**: 652–660.
- Kenward B, Weir AAS, Rutz C, Kacelnik A. 2005.** Tool manufacture by naive juvenile crows. *Nature* **433**: 121–121.
- Kenward B, Rutz C, Weir AAS, Kacelnik A. 2006.** Development of tool use in New Caledonian crows: inherited action patterns and social influence. *Animal Behaviour* **72**: 1329–1343.
- Kutner MH, Nachtsheim CJ, Neter J, Li W. 2004.** *Applied linear statistical models*. Chicago, IL: McGraw-Hill/Irwin.
- Lockman JJ. 2000.** A perception-action perspective on tool use development. *Child Development* **71**: 137–144.
- Seed AM, Tebbich S, Emery NJ, Clayton NS. 2006.** Investigating physical cognition in rooks, *Corvus frugilegus*. *Current Biology* **16**: 697–701.
- Taylor AH, Elliffe D, Hunt GR, Gray RD. 2010.** Complex cognition and behavioural innovation in New Caledonian crows. *Proceedings of the Royal Society of London Series B, Biological Sciences* **277**: 2637–2643.
- Tebbich S, Taborsky M, Fessl B, Blomqvist D. 2001.** Do woodpecker finches acquire tool-use by social learning? *Proceedings of the Royal Society of London Series B, Biological Sciences* **268**: 2189–2193.
- Tebbich S, Seed AM, Emery NJ, Clayton NS. 2007.** Non-tool-using rooks, *Corvus frugilegus*, solve the trap-tube problem. *Animal Cognition* **10**: 225–231.
- Thouless CR, Fanshawe JH, Bertram BCR. 1989.** Egyptian vultures *Neophron percnopterus* and ostrich *Struthio camelus* eggs: the origins of stone-throwing behavior. *Ibis* **131**: 9–15.
- Tinbergen N. 1952.** ‘Derived’ activities; their causation, biological significance, origin, and emancipation during evolution. *Quarterly Review of Biology* **27**: 1–32.
- Tinbergen N. 1963.** On the aims and methods of ethology. *Zeitschrift für Tierpsychologie* **20**: 410–463.
- Weir AAS, Kacelnik A. 2006.** A New Caledonian crow (*Corvus moneduloides*) creatively re-designs tools by bending or unbending aluminium strips. *Animal Cognition* **9**: 317–334.
- Weir AAS, Chappell J, Kacelnik A. 2002.** Shaping of hooks in New Caledonian crows. *Science* **297**: 981.
- Wimpenny JH, Weir AAS, Clayton L, Rutz C, Kacelnik A. 2009.** Cognitive processes associated with sequential tool use in new caledonian crows. *PLoS One* **4**: e6471.