



## Review

# The evolutionary origins and ecological context of tool use in New Caledonian crows

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## ABSTRACT

New Caledonian (NC) crows *Corvus moneduloides* are the most prolific avian tool users. In the wild, they use at least three distinct tool types to extract invertebrate prey from deadwood and vegetation, with some of their tools requiring complex manufacture, modification and/or deployment. Experiments with captive-bred, hand-raised NC crows have demonstrated that the species has a strong genetic predisposition for basic tool use and manufacture, suggesting that this behaviour is an evolved adaptation. This view is supported by recent stable-isotope analyses of the diets of wild crows, which revealed that tool use provides access to highly profitable hidden prey, with preliminary data indicating that parents preferentially feed their offspring with tool-derived food. Building on this work, our review examines the possible evolutionary origins of these birds' remarkable tool-use behaviour. Whilst robust comparative analyses are impossible, given the phylogenetic rarity of animal tool use, our examination of a wide range of circumstantial evidence enables a first attempt at reconstructing a plausible evolutionary scenario. We suggest that a common ancestor of NC crows, originating from a (probably) non-tool-using South-East Asian or Australasian crow population, colonised New Caledonia after its last emersion several million years ago. The presence of profitable but out-of-reach food, in combination with a lack of direct competition for these resources, resulted in a vacant woodpecker-like niche. Crows may have possessed certain behavioural and/or morphological features upon their arrival that predisposed them to express tool-use rather than specialised prey-excavation behaviour, although it is possible that woodpecker-like foraging preceded tool use. Low levels of predation risk may have further facilitated tool-use behaviour, by allowing greater expenditure of time and energy on object interaction and exploration, as well as the evolution of a 'slow' life-history, in which prolonged juvenile development enables acquisition of complex behaviours. Intriguingly, humans may well have influenced the evolution of at least some of the species' tool-oriented behaviours, via their possible introduction of candlenut trees together with the beetle larvae that infest them. Research on NC crows' tool-use behaviour in its full ecological context is still in its infancy, and we expect that, as more evidence accumulates, some of our assumptions and predictions will be proved wrong. However, it is clear from our analysis of existing work, and the development of some original ideas, that the unusual evolutionary trajectory of NC crows is probably the consequence of an intricate constellation of interplaying factors.

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*I watched, without great interest, a crow, ten steps from me, occupied in hunting for [wood-boring beetle larvae] in the trunk of a fallen candlenut tree. . . as the operation drew on, I became more attentive, and perceived a stick held in its beak.*

Le Goupils (1928), translated by Bluff (2008)

## 1. Introduction

For a long time, tool use was widely believed to be a uniquely human trait. This view changed overnight when Jane Goodall reported that chimpanzees at the Gombe Stream, Tanzania, East Africa, use a diversity of tools in foraging and non-foraging contexts (Goodall, 1964; for earlier reports of animal tool use, see Darwin, 1879). Since this discovery, tool use has been observed in an increasing number of animal species (reviews: Beck, 1980; Bentley-Condit and Smith, 2010; Shumaker et al., 2011). Despite this expanding catalogue, however, and the realisation that tool use may not be as 'special' as originally thought (Hansell and Ruxton, 2008), habitual and more sophisticated forms of tool use are noticeably scarce, and largely confined to the great apes and a handful of other species (Shumaker et al., 2011). This phylogenetic rarity raises intriguing questions about the possible evolutionary origins of this behaviour.

We endeavour to gain fresh insights into these issues by investigating a tool-using bird species from a remote tropical island in the South Pacific – the New Caledonian (NC) crow *Corvus moneduloides* (Fig. 1). Given the phylogenetic distance between crows and great apes, there is little doubt that their tool-oriented behaviour has evolved independently. This independence of origin provides a valuable opportunity to investigate the biological circumstances that foster the evolution and maintenance of tool use, as well as its possible dependence on cultural processes. In this review, we focus on the evolution and ecology of tool use in NC crows, leaving aside the question of culture. Some fifty years after Tinbergen (1963) outlined the aims and methods of ethology, his 'four questions' still provide a robust conceptual framework for approaching the task of understanding 'why' an animal exhibits a certain behaviour. Whilst we felt that there is currently insufficient material to discuss the four different levels of explanation – phylogeny, ontogeny, adaptive function, and mechanism – in separate self-contained sections, we kept them very much in mind when writing this paper.

Over the last few decades, research on NC crows, both in the laboratory and in the field, has provided answers to some questions and indicated fruitful avenues for addressing others. Our paper is not meant to be an exhaustive review of the literature on NC crows, let alone of that on the evolution of animal tool use in general. Rather, we have tried to bring together published and unpublished material in a way that allows us to offer some useful speculation on topics where firm evidence is still lacking. We think our piece is best read in the context of earlier reviews on the species' general tool-related behaviour (Hunt and Gray, 2006), and the possible cognitive mechanisms underlying it (Kacelnik et al., 2006; Bluff et al., 2007).



**Fig. 1.** A New Caledonian (NC) crow uses a (non-hooked) stick tool (A) to extract a beetle larva from its burrow in a candlenut stump (B). Note that the tool remains inserted after successful deployment. Tools that are left behind at foraging sites are sometimes 'adopted' by other crows, and can be collected by researchers for closer examination. For further information on NC crows' 'larva-fishing' behaviour, see the main text and Fig. 5. Photos: J. Troscianko; reproduced from Fig. S1 in Rutz et al. (2010).

## 2. Tool-use behaviour in the wild

### 2.1. Current distribution and habitats

NC crows are endemic to the remote Pacific archipelago of New Caledonia, inhabiting the main island, Grande Terre, as well as one of the sister islands, Maré (Fig. 2). Delacour (1966) asserts that NC crows were introduced by humans to Maré (subsequently cited by several other authors, including Doughty et al., 1999; Hunt and Gray, 2003; del Hoyo et al., 2009), but since he failed to provide convincing supporting evidence, we consider this claim contentious. A smaller population on another sister island, Lifou, which was also possibly due to introduction by humans (Barré and Dutson, 2000), is apparently now extinct (unpubl. data; Dutson, 2011).

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