Russell Gray - selected references

1 Taylor, A. H., Cheke, L. G., Waismeyer, A., Meltzoff, A. N., Miller, R., Gopnik, A. et al. (2014). Of babies and birds: complex tool behaviours are not sufficient for the evolution of the ability to create a novel causal intervention. *Proc.Biol.Sci., 281*.
Notes: Humans are capable of simply observing a correlation between cause and effect, and then producing a novel behavioural pattern in order to recreate the same outcome. However, it is unclear how the ability to create such causal interventions evolved. Here, we show that while 24-month-old children can produce an effective, novel action after observing a correlation, tool-making New Caledonian crows cannot. These results suggest that complex tool behaviours are not sufficient for the evolution of this ability, and that causal interventions can be cognitively and evolutionarily disassociated from other types of causal understanding

2 Logan, C. J., Jelbert, S. A., Breen, A. J., Gray, R. D., & Taylor, A. H. (2014). Modifications to the Aesop's Fable paradigm change New Caledonian crow performances. *PLoS.ONE., 9,* e103049.
Notes: While humans are able to understand much about causality, it is unclear to what extent non-human animals can do the same. The Aesop's Fable paradigm requires an animal to drop stones into a water-filled tube to bring a floating food reward within reach. Rook, Eurasian jay, and New Caledonian crow performances are similar to those of children under seven years of age when solving this task. However, we know very little about the cognition underpinning these birds' performances. Here, we address several limitations of previous Aesop's Fable studies to gain insight into the causal cognition of New Caledonian crows. Our results provide the first evidence that any non-human animal can solve the U-tube task and can discriminate between water-filled tubes of different volumes. However, our results do not provide support for the hypothesis that these crows can infer the presence of a hidden causal mechanism. They also call into question previous object-discrimination performances. The methodologies outlined here should allow for more powerful comparisons between humans and other animal species and thus help us to determine which aspects of causal cognition are distinct to humans

3 Jelbert, S. A., Taylor, A. H., Cheke, L. G., Clayton, N. S., & Gray, R. D. (2014). Using the Aesop's fable paradigm to investigate causal understanding of water displacement by New Caledonian crows. *PLoS.ONE., 9,* e92895.
Notes: Understanding causal regularities in the world is a key feature of human cognition. However, the extent to which non-human animals are capable of causal understanding is not well understood. Here, we used the Aesop's fable paradigm--in which subjects drop stones into water to raise the water level and obtain an out of reach reward--to assess New Caledonian crows' causal understanding of water displacement. We found that crows

preferentially dropped stones into a water-filled tube instead of a sand-filled tube; they dropped sinking objects rather than floating objects; solid objects rather than hollow objects, and they dropped objects into a tube with a high water level rather than a low one. However, they failed two more challenging tasks which required them to attend to the width of the tube, and to counter-intuitive causal cues in a U-shaped apparatus. Our results indicate that New Caledonian crows possess a sophisticated, but incomplete, understanding of the causal properties of displacement, rivalling that of 5-7 year old children

4 Taylor, A. H., Miller, R., & Gray, R. D. (2012). New Caledonian crows reason about hidden causal agents. *Proceedings of the National Academy of Sciences of the United States of America, 109,* 16389-16391.
Notes: The ability to make inferences about hidden causal mechanisms underpins scientific and religious thought. It also facilitates the understanding of social interactions and the production of sophisticated tool-using behaviors. However, although animals can reason about the outcomes of accidental interventions, only humans have been shown to make inferences about hidden causal mechanisms. Here, we show that tool-making New Caledonian crows react differently to an observable event when it is caused by a hidden causal agent. Eight crows watched two series of events in which a stick moved. In the first set of events, the crows observed a human enter a hide, a stick move, and the human then leave the hide. In the second, the stick moved without a human entering or exiting the hide. The crows inspected the hide and abandoned probing with a tool for food more often after the second, unexplained series of events. This difference shows that the crows can reason about a hidden causal agent. Comparative studies with the methodology outlined here could aid in elucidating the selective pressures that led to the evolution of this cognitive ability

5 Taylor, A. H., Hunt, G. R., & Gray, R. D. (2012). Context-dependent tool use in New Caledonian crows. *Biol.Lett., 8,* 205-207.
Notes: Humans and chimpanzees both exhibit context-dependent tool use. That is, both species choose to use tools when food is within reach, but the context is potentially hazardous. Here, we show that New Caledonian crows used tools more frequently when food was positioned next to a novel model snake than when food was positioned next to a novel teddy bear or a familiar food bowl. However, the crows showed no significant difference in their neophobic reactions towards the teddy bear and the model snake. Therefore, the crows used tools more in response to a risky object resembling a natural predator than to a less-threatening object that provoked a comparable level of neophobia. These results show that New Caledonian crows, like humans and chimpanzees, are capable of context-dependent tool use

6 Taylor, A. H., Knaebe, B., & Gray, R. D. (2012). An end to insight? New Caledonian crows can spontaneously solve problems without planning their actions. *Proc.Biol.Sci., 279,* 4977-4981.
Notes: Animals rarely solve problems spontaneously. Some bird species, however, can immediately find a solution to the string-pulling problem. They are able to rapidly gain access to food hung on the end of a long string by repeatedly pulling and then stepping on the string. It is currently unclear whether these spontaneous solutions are produced by insight or by a perceptual-motor feedback loop. Here, we presented New Caledonian crows and humans with a novel horizontal string-pulling task. While the humans succeeded, no individual crow showed a significant preference for the connected string, and all but one failed to gain the food even once. These results clearly show that string pulling in New Caledonian crows is generated not by insight, but by perceptual feedback. Animals can spontaneously solve problems without planning their actions

7 Abdelkrim, J., Hunt, G. R., Gray, R. D., & Gemmell, N. J. (2012). Population genetic structure and colonisation history of the tool-using New Caledonian crow. *PLoS.ONE., 7,* e36608.
Notes: New Caledonian crows exhibit considerable variation in tool making between populations. Here, we present the first study of the species' genetic structure over its geographical distribution. We collected feathers from crows on mainland Grande Terre, the inshore island of Toupeti, and the nearby island of Mare where it is believed birds were introduced after European colonisation. We used nine microsatellite markers to establish the genotypes of 136 crows from these islands and classical population genetic tools as well as Approximate Bayesian Computations to explore the distribution of genetic diversity. We found that New Caledonian crows most likely separate into three main distinct clusters: Grande Terre, Toupeti and Mare. Furthermore, Toupeti and Mare crows represent a subset of the genetic diversity observed on Grande Terre, confirming their mainland origin. The genetic data are compatible with a colonisation of Mare taking place after European colonisation around 1900. Importantly, we observed (1) moderate, but significant, genetic differentiation across Grande Terre, and (2) that the degree of differentiation between populations on the mainland increases with geographic distance. These data indicate that despite individual crows' potential ability to disperse over large distances, most gene flow occurs over short distances. The temporal and spatial patterns described provide a basis for further hypothesis testing and investigation of the geographical variation observed in the tool skills of these crows

8 Taylor, A. H., Elliffe, D., Hunt, G. R., & Gray, R. D. (2010). Complex cognition and behavioural innovation in New Caledonian crows. *Proc.Biol.Sci., 277,* 2637-2643.
Notes: Apes, corvids and parrots all show high rates of behavioural innovation in the wild. However, it is unclear whether this innovative behaviour is

underpinned by cognition more complex than simple learning mechanisms. To investigate this question we presented New Caledonian crows with a novel three-stage metatool problem. The task involved three distinct stages: (i) obtaining a short stick by pulling up a string, (ii) using the short stick as a metatool to extract a long stick from a toolbox, and finally (iii) using the long stick to extract food from a hole. Crows with previous experience of the behaviours in stages 1-3 linked them into a novel sequence to solve the problem on the first trial. Crows with experience of only using string and tools to access food also successfully solved the problem. This innovative use of established behaviours in novel contexts was not based on resurgence, chaining and conditional reinforcement. Instead, the performance was consistent with the transfer of an abstract, causal rule: 'out-of-reach objects can be accessed using a tool'. This suggests that high innovation rates in the wild may reflect complex cognitive abilities that supplement basic learning mechanisms

9 Taylor, A. H., Medina, F. S., Holzhaider, J. C., Hearne, L. J., Hunt, G. R., & Gray, R. D. (2010). An investigation into the cognition behind spontaneous string pulling in New Caledonian crows. *PLoS.ONE., 5,* e9345.
Notes: The ability of some bird species to pull up meat hung on a string is a famous example of spontaneous animal problem solving. The "insight" hypothesis claims that this complex behaviour is based on cognitive abilities such as mental scenario building and imagination. An operant conditioning account, in contrast, would claim that this spontaneity is due to each action in string pulling being reinforced by the meat moving closer and remaining closer to the bird on the perch. We presented experienced and naive New Caledonian crows with a novel, visually restricted string-pulling problem that reduced the quality of visual feedback during string pulling. Experienced crows solved this problem with reduced efficiency and increased errors compared to their performance in standard string pulling. Naive crows either failed or solved the problem by trial and error learning. However, when visual feedback was available via a mirror mounted next to the apparatus, two naive crows were able to perform at the same level as the experienced group. Our results raise the possibility that spontaneous string pulling in New Caledonian crows may not be based on insight but on operant conditioning mediated by a perceptual-motor feedback cycle

10 Mehlhorn, J., Hunt, G. R., Gray, R. D., Rehkamper, G., & Gunturkun, O. (2010). Tool-making new caledonian crows have large associative brain areas. *Brain,Behavior and Evolution, 75,* 63-70.
Notes: Animals with a high rate of innovative and associative-based behavior usually have large brains. New Caledonian (NC) crows stand out due to their tool manufacture, their generalized problem-solving abilities and an extremely high degree of encephalization. It is generally assumed that this increased brain size is due to the ability to process, associate and memorize diverse stimuli, thereby enhancing the propensity to invent new and complex

behaviors in adaptive ways. However, this premise lacks firm empirical support since encephalization could also result from an increase of only perceptual and/or motor areas. Here, we compared the brain structures of NC crows with those of carrion crows, jays and sparrows. The brains of NC crows were characterized by a relatively large mesopallium, striatopallidal complex, septum and tegmentum. These structures mostly deal with association and motor-learning. This supports the hypothesis that the evolution of innovative or complex behavior requires a brain composition that increases the ability to associate and memorize diverse stimuli in order to execute complex motor output. Since apes show a similar correlation of cerebral growth and cognitive abilities, the evolution of advanced cognitive skills appears to have evolved independently in birds and mammals but with a similar neural orchestration

11 Holzhaider, J. C., Hunt, G. R., & Gray, R. D. (2010). Social learning in New Caledonian crows. *Learn.Behav., 38,* 206-219.
Notes: New Caledonian (NC) crows are the most sophisticated tool manufacturers other than humans. The diversification and geographical distribution of their three Pandanus tool designs that differ in complexity, as well as the lack of ecological correlates, suggest that cumulative technological change has taken place. To investigate the possibility that high-fidelity social transmission mediated this putative ratchet-like process, we studied the ontogeny of Pandanus tool manufacture and social organization in free-living NC crows. We found that juvenile crows took more than 1 year to reach adult proficiency in their Pandanus tool skills. Although trial-and-error learning is clearly important, juveniles have ample opportunity to learn about Pandanus tool manufacture by both observing their parents and interacting with artifactual material. The crows' social system seems likely to promote the faithful social transmission of local tool designs by both favoring the vertical transmission of tool information and minimizing horizontal transmission. We suggest that NC crows develop their Pandanus tool skills in a highly scaffolded learning environment that facilitates the cumulative technological evolution of tool designs

12 Hunt, G. R. & Gray, R. D. (2004). The crafting of hook tools by wild New Caledonian crows. *Proc.Biol.Sci., 271 Suppl 3,* S88-S90.
Notes: The 'crafting' of tools involves (i) selection of appropriate raw material, (ii) preparatory trimming and (iii) fine, three-dimensional sculpting. Its evolution is technologically important because it allows the open-ended development of tools. New Caledonian crows manufacture an impressive range of stick and leaf tools. We previously reported that their toolkit included hooked implements made from leafy twigs, although their manufacture had never been closely observed. We describe the manufacture of 10 hooked-twig tools by an adult crow and its dependent juvenile. To make all 10 tools, the crows carried out a relatively invariant three-step sequence of complex manipulations that involved (i) the selection of raw material, (ii) trimming and (iii) a lengthy sculpting of the hook. Hooked-twig manufacture

contrasts with the lack of sculpting in the making of wooden tools by other non-humans such as chimpanzees and woodpecker finches. This fine, three-stage crafting process removes another alleged difference between humans and other animals

13 Hunt, G. R. & Gray, R. D. (2003). Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proc.Biol.Sci., 270,* 867-874.
Notes: Many animals use tools but only humans are generally considered to have the cognitive sophistication required for cumulative technological evolution. Three important characteristics of cumulative technological evolution are: (i) the diversification of tool design; (ii) cumulative change; and (iii) high-fidelity social transmission. We present evidence that crows have diversified and cumulatively changed the design of their pandanus tools. In 2000 we carried out an intensive survey in New Caledonia to establish the geographical variation in the manufacture of these tools. We documented the shapes of 5550 tools from 21 sites throughout the range of pandanus tool manufacture. We found three distinct pandanus tool designs: wide tools, narrow tools and stepped tools. The lack of ecological correlates of the three tool designs and their different, continuous and overlapping geographical distributions make it unlikely that they evolved independently. The similarities in the manufacture method of each design further suggest that pandanus tools have gone through a process of cumulative change from a common historical origin. We propose a plausible scenario for this rudimentary cumulative evolution