between the geographic distribution of favorable habitats and dispersibility nonetheless greatly influence how species interact with each other, how and to what extent speciation occurs, and the kinds of adaptations that are likely to evolve. Biodiversity is more than counting species; it is about understanding interactions, phenotypes, and evolutionary processes in a heterogeneous biosphere.

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Further reading

- Benton, M.J. (2001). Biodiversity on land and in the sea. Geol. J. 36, 211–230.
- Boyce, C.K., and Zwieniecki, M.A. (2012). Leaf fossil record suggests limited influence of atmospheric CO₂ on terrestrial productivity prior to angiosperm evolution. Proc. Natl. Acad. Sci. USA 109, 10403–10408.
- Carrete Vega, G., and Wiens J.J, (2012). Why are there so few fish in the sea? Proc. Roy. Soc. B 279, 2323–2329.
- Denny, M.W. (1993). Air and Water: The Biology and Physics of Life's Media (Princeton: Princeton University Press).
- Friedman, M. (2010). Explosive morphological diversification of spiny-finned teleost fishes in the aftermath of the end-Cretaceous extinction. Proc. Roy. Soc. B 277, 1675–1683.
- Logares, R., Brate, J., Bertilsson, S., Clasen, J.L., Shalchlian-Tabrizi, K., and Regefors, K. (2009). Infrequent marine-freshwater transitions in the microbial world. Trends Microbiol. 17, 414-422.
- May, R.M. (1994). Biological diversity: differences between land and sea. Phil. Trans. Roy. Soc. Lond. B 343, 105–111.
- Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B., and Worm, B. (2011). How many species are there on Earth and in the ocean? PLoS Biol. 9 e1001127.
- Schmidt-Nielsen, K. (1972). Locomotion: energy cost of swimming, flying, and running. Science 177, 222–228.
- Strathmann, R.R. (1990). Why life histories evolve differently in the sea. Am. Zool. 30, 197–207.
- Vermeij, G.J., and Dudley, R. (2000). Why are there so few evolutionary transitions between aquatic and terrestrial ecosystems? Biol. J. Linn. Soc. 70, 541-554.
- Vermeij, G.J. and Grosberg, R.K. (2010). The great divergence: when did diversity on land exceed that in the sea? Integr. Comp. Biol. 50, 675-682.

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Spontaneous innovation in tool manufacture and use in a Goffin's cockatoo

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Accounts of complex tool innovations in animals, particularly in species not adaptively specialized for doing so, are exceedingly rare and often linked to advanced cognitive abilities in the physical domain [1], even though the relation between such capabilities and intelligence is poorly understood [2]. For this reason, discoveries of such capabilities transcend anecdotal value and contribute significantly to comparative cognition [3-5]. Among birds, there are several reports of tool innovations in corvids, but very few documented records in other families (for example [1,3-7]). Here, we report a case of spontaneous tool innovation in the Goffin's cockatoo (Cacatua goffini). a species endemic to the Tanimbar archipelago in Indonesia. Like most corellas, they live in social groups (~10-100) in tropical dry forests, roost in simple tree holes, and feed mainly on a seed based diet (which occasionally causes interference with agriculture) [8]. There are no records of tool-related behavior in the wild. We report how a captive male named Figaro successfully, reliably and repeatedly made and used stick-type tools to rake in food, manufacturing them from two different materials and displaying different steps and techniques.

During apparently playful explorations, Figaro inserted a stone pebble through the aviary wire mesh, where it fell on a structural wooden beam. After attempting to reach the pebble with his claw, he went away, fetched a piece of bamboo, returned, and used it to fish (unsuccessfully) for the stone, adjusting the movement of the functional tool-end to the movement of the pebble. To follow this serendipitous observation we

placed cashew nuts where the pebble had been, in 10 trials over three days. Testing took place in visual isolation from the group, but (to avoid the stress of isolation) in the company of Heidi, a submissive female.

In the first test, after trying an undersized stick from the aviary's floor, Figaro started breaking a large splinter off the beam (European larch, which had previously been left untouched by the animals), using his beak through the wire mesh. Heidi joined in for the last cut, but Figaro chased her away and finally got hold of the splinter by threading it in through the mesh. He immediately started to use it to rake in the nut. Occasionally the nut fell off the distal side of the beam, and we repositioned it. The curved bill forced the bird to work diagonally downwards to see the movement of the reward (see Supplemental Movie S1). Figaro combined straight pulls (placing the tool's end behind the nut and pulling it towards him) and sideward levering movements against the grid. He used 10 tools in 10 trials, nine of which were manufactured and one ready-made (Figure 1A).

Time for manufacture improved across trials, indicative of learning, but, notably, improvement was not gradual: the first attempt took nearly 25 minutes, but afterwards the mean time for manufacture was short and stable (excluding the first test, $X \pm SE = 2:27\pm0:34$; Figure 1B). Except for tool T6, which was initially too long (Figaro halved it following one ineffective raking attempt), the splinters were cut off at their final, suitable length (Figure S1 in the Supplemental Information). T9 was a piece of bamboo from the aviary's floor. T10's manufacturing was complex, involving four cuts to a branching twig on the aviary floor (Figure 1C). The first cut (cut 1) was discarded; he then (cut 2) removed a large side arm from near the twig's stem by stepping on the stem whilst twisting off the sidearm with his beak. Figaro tried the entire side arm first, but after an unsuccessful insertion attempt shortened the remaining first by a third (cut 3) and finally cut the remaining part in half (cut 4). He used the resulting distal piece successfully to retrieve the food.

We tested another male, Pipin, and Heidi in the same situation. Pipin did not try to use tools, but Heidi,

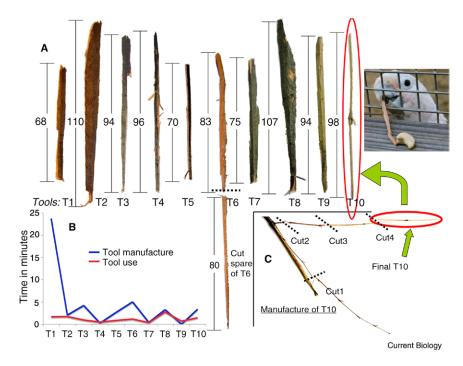


Figure 1. Manufacture and use of tools 1-10. (A) Tools used (T1-T10); tool length in mm; T1-T8 = splinter tools; T9 = bamboo tool; T10 = twig tool. (B) Blue: time for tool manufacture; red: time for tool use (from manufacture to retrieval) for each trial in minutes. (C) Manufacture of T10 using four sequential cuts.

who had witnessed Figaro's tests, (unsuccessfully) showed components of the behavior, breaking off small chips of wood and inserting them through the mesh. Like Figaro's, Heidi's attempts were not shaped by direct reinforcement, but could either have reflected her social experience with Figaro or independent attempts at the same solution.

Several added factors make Figaro's performance interesting. First, his raking actions were particularly challenging because the tool movements were constantly adjusted to the shifting position of the target, and impeded by the mesh. Second, the comparison with corvids is instructive. Among corvids, blue jays ripping pieces of newspaper to rake in food pellets provide an earlier example of similar innovation by a non-tool user [5]. Parrots and corvids are unlikely to share tool-using ancestors, but being equally notable in terms of learning, brain size and anatomy [9] both provide an arena to test hypotheses for the evolution of different aspects of intelligence. Most corvids, however, are nest builders and have straight beaks, while most parrots are cavity

nesters and have curved beaks that impede easy holding of stick-type tools as prolongations of the beak [6]. Thus, Figaro overcame various morphological (beak curvature, tool held against upper mandible with tongue), ecological (the species is unknown to use tools and nests in cavities) and situational (splinter tools cut and used through the mesh) constraints, making his performance difficult to explain in terms of recombination of conventionally acquired, previously reinforced behaviours [10].

Our observations prove that innovative tool-related problem-solving is within this species' cognitive resources. As it is unknown for tools to play a major role in this species' ecology, this strengthens the view that tool competences can originate on general physical intelligence, rather than just as problem-specific ecological solutions (see discussions in [2,4]). The precise cognitive operations underlying such innovations are still unknown, but future studies may continue to unravel them by modifying the tasks, and controlling the developmental history and

pre-experimental experience across different groups of subjects.

Supplemental Information

Supplemental Information includes experimental procedures, one Figure and one Movie and can be found with this article online at http://dx.doi.org/10.1016/ i.cub.2012.09.002.

References

- 1. Shumaker, R.W., Walkup, K.R., and Beck, B. (2011). Animal Tool Behavior: The Use and Manufacture of Tools by Animals, revised and updated edition (Baltimore: The Johns Hopkins University Press).
- Kacelnik, A. (2009). Tools for thoughts or thoughts for tools? Proc. Natl. Acad. Sci. USA 106, 10071-10072.
- Weir, A., Chappell, J., and Kacelnik, A. (2002). Shaping of hooks in New Caledonian crows. Science 297, 981.
- 4. Bird, C., and Emery, N.J. (2009). Insightful problem solving and creative tool modification by captive nontool-using rooks. Proc. Natl. Acad. Sci. USA 106, 10370-10375
- Jones, T.B., and Kamil, A.C. (1973). Toolmaking and tool-using in the Northern blue jay. Science 180, 1076-1078.
- Auersperg, A.M.I., von Bayern, A.M.P, Gajdon, G.K., Huber, L., and Kacelnik, A (2011). Flexibility in problem solving and tool use of kea and New Caledonian crows in a Multi Access Box paradigm, PLoS One 6. e20231.
- 7. Borsari, A., and Ottoni, E.B. (2005). Preliminary observations of tool use in captive hyacinth macaws (Anodorhynchus hyacinthinus). Anim. Cogn. 8, 48-52.
- 8. Jepson, P., Brickle, N., and Chayadin, Y. (2001). The conservation status of Tanimbar corella and bluestreaked lory on the Tanimbar Islands, Indonesia: results of a rapid contextual survey. Oryx 35, 224-233.
- Striedter, G.F. (2005). Principles of Brain Evolution. (Sinauer Associates, Sunderland,
- Epstein, R., Kirshnit, C.E., Lanza, R.P., and Rubin, L.C. (1984). "Insight" in the pigeon: Antecedents and determinants of an intelligent performance. Nature 308, 61-62.

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