

state and at a private university. Despite the great diversity among them, there is a common theme. All universities have flaws, but the ideal is a universal one, a place where scholars are free to study and teach, and young people to learn. Robert Maynard Hutchins was chancellor of the University of Chicago when I was an undergraduate student. At the time, Senator Joseph McCarthy was attacking liberals as subversive, and his attacks represented a serious challenge to the freedom of all universities. Hutchins would have none of it. He said that “No University of Chicago professor will be fired for any reason short of rape or murder committed at high noon with three witnesses.”

What were some of the best times in your scientific life? I spent a year in the Physiology Department at Oxford in 1971–72. David Whitteridge, the chairman of the department, became a close friend. Early on in my time there he knocked on John Stein’s door and said; “You two might have something to discuss”. We did, and we still do. John and I began looking for, and then recording visual responses of cells in the pontine nuclei. The collaboration was enriched the next year after I returned to Brown University by the good fortune of the arrival of two outstanding young people. Alan Gibson arrived as a postdoc, sent on by Mike Gazzaniga, and Jim Baker as a graduate student encouraged to come to Brown by Mark Berkley. All four were equally intelligent, but each of us had a unique contribution. Mine was to be the vague philosopher of the group, John Stein, the enthusiastic spark plug. Alan Gibson was the creative lab person, and Jim the deeply thoughtful critic. A very lucky combination. John Stein would come Summers to continue to work with us, and later, George Mower and Ric Robinson came to continue to study other visual inputs to the pons and cerebellum.

What are your views on international collaboration in science? When I started working in labs we were often only dimly aware of contributions from foreign labs. Over the years the scientific community became a global one. You began to know your colleagues and to understand them as people. You began to make friends across international borders, and know your colleagues as

close friends, and the names and the career plans of their children.

Which of the papers you have written was the most fun? At Brown, we had a weekly vision lunch where we would discuss new papers, old questions, or sports cars. When we discussed how to determine the focal plane of an eye, it was agreed that you must use a retinoscope. The observer moves the light source back and forth and looks at a shadow reflected from the back of the eye. Ross Beauchamp, one of Lorrin Riggs’ graduate students asked “What if the retinoscope reflects from a layer other than the receptors?” No one had a ready answer, but it didn’t seem like it would give much of an error. It does. The retina of all mammals is roughly equal in thickness, from the 2 mm diameter eye of a small brown bat to the 50 mm eye of a baleen whale. Because the plane reflecting the light and shadow is at a roughly constant distance from the receptors, I could calculate the error which would be due to reflection from a surface in front of or behind the rods and cones. The calculated error is a function of the inverse square of the focal length. Michel Millodot and I collected data from the literature and refracted the eyes of several animals varying in size. Mice appeared to be 15 diopters hypermetropic, rats seven diopters, and rabbits two. All of these readings are due to errors of the reflecting surface being at a plane in front of the receptors. The fun was in first calculating the nature of the error, and then finding it.

Why do you think that some scientists prosper while others of equal ability do not? Unfortunately, it often relates to the extent to which they are skilled at self-promotion. Most of us know people of great intellect and skill who are virtually unknown outside their institution. We also usually know scientists who seem to rise high in the field for no obvious reason except for their talent for self-promotion. I learned scepticism from Roger Sperry. If I got excited about a colleague and suggested we invite him or her to speak Roger would growl; “What has he discovered?” Fair enough.

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Quick guides

Nest building by birds

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What is a bird nest like? Bird nests vary enormously among species in their form, size and composition. The nest of a long-tailed tit (*Aegithalos caudatus*) is a flexible bag composed of small-leaved mosses entangled in myriad loops of fluffy spider egg cocoon silk — a ‘Velcro’ fabric. For insulation, this bag is lined with as many as 2,000 small feathers. For camouflage, the outside of the nest is covered with a few thousand small lichen flakes. At the other extreme of nest complexity is the nest of the Arctic tern (*Sterna paradisea*), which is often no more than a shallow depression scraped in a shingle beach. The size of nests is equally variable. An Antillean crested hummingbird (*Orthorhyncus cristatus*), at ~2.4 grams, may be more than twice the weight of the tiny nest cup on which it sits, while the massive platform nest of the bald eagle (*Haliaeetus leucocephalus*) can be three metres in width and weigh up to three metric tons, about 600 times the weight of the bird itself. The composition of nesting material varies from grasses and twigs (Figure 1) to those used by the common tailorbird (*Orthotomus sutorius*), which stitches together a folded-over living leaf with threads of spider silk.

What is a nest for? Nests are structures built, or modified, to provide some security from the hazards of the world outside. They are built by a wide range of animals, including many insects. Among the vertebrates there are some fish and reptile species that build nests and some mammals, but nest building of some kind is almost universal among birds.

The sole function of nests built by virtually all bird species is to raise young. In many species, however, for example waterfowl and gamebirds, chicks leave the nest soon after hatching, so the nest is built simply to protect the eggs during incubation. There are few exceptions to the reproductive function of nests in birds.



Figure 1. The nest of the crossbill *Loxia curvirostra* has a distinctive structure and several components.

The base of the cup is made of pine twigs, built up with grasses, moss and lichen and lined with fine grass and feathers. How complex is this to build? (Photo courtesy of Robert Rae.)

One is the white-breasted wood wren (*Henicorhina leucostica*), from the forests of Central and South America, which builds a smaller, thinner-walled version of its breeding nest as a night roost throughout the year.

Does nest building require 'complex cognition'? To build a nest such as that of the village weaver — a hanging hollow globe of green grass complete with entrance porch — requires a suite of decisions concerning a suitable location for the nest site, the materials to use (substance, size, shape, malleability, strength), and the construction behaviour itself. It may also require collaboration between partners as often the outer structure is built by the male and then lined by a female. In some species, including the long-tailed tit, the structure from start to finish requires collaboration between a pair of birds. All of these requirements suggest a significant planning capacity, behavioural flexibility and manipulative skill.

Similarly in hominids, the increased capability for making and using tools, allowed by the evolution of bipedalism freeing the hands, led to a

greater potential for control over the environment, stimulating, it has been suggested, social co-operation and the development of language. This is believed to account for the rapid expansion of brain size in hominid evolution over the last three million years. Tool construction and use is not confined to the great apes and hominids but is also a feature of the behavioural repertoire of several bird species, in particular, the Galapagos woodpecker finch (*Cactospiza pallida*) and the New Caledonian crow (*Corvus moneduloides*).

Just as tool manufacture is common to humans and to birds, so song in songbirds is often considered to be a kind of language and song development, at least, exhibits similarities with language development in children. Therefore, some bird species share with humans two types of behaviour, song development and tool manufacture and use, thought to require complex cognition. It seems plausible that nest building by some bird species, at least, similarly shares complex cognitive requirements. It has been pointed out, for example, that string bag making by the Telefol women

in New Guinea, learned by young girls from their mothers, has a complexity of design and need for manual dexterity comparable to that of the nest building of village weavers.

Do birds learn to build nests? The classic method of demonstrating that there is a learned component to a behaviour has been the 'deprivation experiment': does an animal deprived of an experience while growing up nevertheless perform the behaviour perfectly the first time it has the opportunity? Amazingly, such an experiment was apparently carried out by the English naturalist John Ray in the 17th century, since he writes of birds building their nests: "and this they do though they never saw nor could see any nest made, that is though taken from the nest and brought up by hand". The next such study did not take place until the 1960s when deprivation experiments carried out on village weavers (*Ploceus cucullatus*) showed that effective weaving of the grass strands that make up the nest depended substantially upon building experience. In the subsequent years, virtually no further work has been done to establish the extent and nature of the learning processes involved in the nest building of this or any other species.

In spite of the number and ubiquity of birds' nests, we know little of the cognitive processes that might be involved in their construction (Figure 2). Although there is enough similarity in nest design for a nest collector to recognise which species built a nest, we do not know how a bird knows what nest shape/size to build. There are several, increasingly complex possibilities. Each of these possibilities may explain how other kinds of complex cognition, such as song learning, appear and develop. The simplest possibility is that the bird has no concept of what it is aiming to produce but has a set of rules for its behaviour, which if followed in appropriate order lead to the emergence of a nest.

It is possible that a bird comes into the world with a template that provides the basic information as to what a nest should be like and how it should be constructed, but uses feedback during the construction process to improve building performance. This might explain what appears to be practice nest building by the village weaver. One might expect that a young bird, having learned how to build a nest, would then



Figure 2. A series of nests, or part nests, built by a single mistle thrush *Turdus viscivorus*.

Von Frisch saw this kind of behaviour as a bird being muddled by topographic similarity and, although it might see the multiple nests, its mind is unable to make a suitable response. Is this evidence for the apparent complexity of nest building being entirely represented by the genome? (Photo courtesy of R. Downer.)

continue to build very similar nests just as 'closed-ended' song learners that learn songs only in their first year of life do not subsequently change their songs. Where this is the case, one should expect nests of the same species to be very similar with as much variation within a bird as among birds. Although young weaver birds take longer and build less effective nests than do experienced birds, it is not clear whether experience continues to be accumulated once the birds are mature.

It is not out of the question that birds learn about nest materials and construction while in the nest, just as they imprint on their siblings and parents so as to stick to mother while young and vulnerable, and to mate with the appropriate mate when sexually mature. This process has sufficient plasticity that young birds may imprint on any moving object, as was memorably demonstrated by Konrad Lorenz, whose hand-raised goslings both followed, and later attempted to mate with, his Wellington boots. Cross-fostering experiments would help to determine whether or not birds acquire information during early development in a way that is akin to imprinting. Alternatively, one would expect to see significant similarity between the nests built by parents and offspring.

The most cognitively sophisticated scenario is one in which learning would underpin all, or nearly all, of the nest building process, from choice of suitable sites for placement and suitable materials to how to put those materials together. One would expect to see not only practice nests in young birds but continuing evidence for experience modifying nest manufacture and quality throughout adult life. Additionally, one might expect to see a bird, presented with a nest that has been experimentally damaged in an unusual way, repair it in the most direct and economic way, as if it had a concept of the completed structure. Such an experiment was conducted in the 1950s on a wild population of baya weavers (*Ploceus phippipinus*), but the results were very variable and difficult to interpret.

Implications for models of complex cognition. The value of understanding complex cognition in birds has been long and amply demonstrated by the vast and increasingly sophisticated work on song learning. The mechanisms for understanding song may also be helpful in addressing the role of cognition in nest building. If nest building requires at least some kind of 'complex' cognition this may mean a fundamental reappraisal of the significance of tool use and manufacture is required. While investigations of tool use in birds have recently been employed as model systems in the study of complex cognition, the value of tools in such studies is somewhat limited by their rarity. The accessibility of the behaviour of nest building, its wide variation and its sheer ubiquity make this behaviour enormously promising as a successor to song learning as an instrument/tool for understanding not only complex cognition in birds but also for other vertebrates, even ourselves.

Where can I find out more?

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ADF/Cofilin

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Also known as... actophorin (amoeba), Dcof (*Dictyostelium discoideum*), depactin (*Asterias amurensis*, i.e., starfish), destrin (ADF in mammals), cofilin-1 (isoform found in non-muscle tissue and called nm-cofilin), cofilin-2 (isoform first identified in muscle and called m-cofilin), Twinstar (*Drosophila melanogaster*), UNC60A and UNC60B (*Caenorhabditis elegans*).

What are ADF and cofilin and how do they differ structurally?

The first member of this family, actin-depolymerizing factor (ADF), was isolated in 1980 from embryonic chick brain and named for its ability to depolymerize low concentrations of filamentous actin (F-actin) to monomeric actin (G-actin). Cofilin-1 was isolated 4 years later from porcine brain and named for its ability to bind and co-sediment with F-actin (co-filamentous with actin). Further characterization showed that both ADF and cofilin-1 could enhance subunit turnover in F-actin. They bind and sever F-actin and, under some conditions, they increase the G-actin pool. ADF and cofilin from the same species have about 70% amino-acid sequence identity, but human ADF has only 59% identity with *Xenopus* ADF/cofilin and only 27% identity with *Drosophila* Twinstar.

Where are they found? Every eukaryotic cell expressing actin also expresses one or more members of this family. Unicellular eukaryotes express only a single member, whereas metazoans express multiple forms. Vertebrates express ADF, cofilin-1 and cofilin-2. Some higher plants, such as *Arabidopsis thaliana*, express 10 isoforms named ADF-1 to ADF-10. It is not clear which plant ADFs, if any, have behaviors similar to either animal ADF or cofilin.

What do they do? ADF/cofilin family members enhance the cycling of subunits through the filament by binding to a slightly twisted form of F-actin, thus stabilizing the twisted state, enhancing severing and providing more filament ends (Figure 1).