of meristem function, but may be dispensable in organ primordia where the main emphasis may be on a maximal growth rate.

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Animal Cognition: The Trade-off to Being Smart

Great tits that learn to manipulate a device to obtain food in the laboratory go on to lay more eggs in the wild. However, the solver great tits are also more likely to desert their nest.

Susan D. Healy

Most of us think it pays to be smart. After all, surely that is the reason that humans are, arguably, the most dominant species on our planet, and certainly the one having the most significant impact. We know that we are really smart, not just because we have one of the largest brains (relative to body size) of any extant animal, but because we are also remarkable innovators and problem solvers. It may seem surprising, then, that the work reported in this issue of *Current Biology* by Cole *et al.* [1] is, to my knowledge, the first concrete evidence that problem-solving abilities might have positive fitness benefits. Cole *et al.* [1] show that smart is good by discovering that adult great tits that learn how to access food from a novel man-made food container go on to lay more eggs than those birds that fail to solve this problem. These parents also spend less time foraging for their young. What good news, the smart can afford to be lazy, too!

If the benefits to being smart are all too obvious, why has it taken so long for anyone to collect convincing data confirming the fitness benefits? In part, this is likely to be because few have thought it worth the bother to check. After all, we have daily proof of our own ingenuity and its value. Additionally, the researchers who are typically the most interested in cognitive abilities are most interested in understanding the mechanisms underpinning what animals can learn and remember: that work often does not easily lend itself to helping to determine whether better task performance is beneficial to the subject outside the context of the experiment or what those benefits might be (especially if the experimental context is very controlled or contrived). Moreover, measuring fitness benefits of a given trait in the real world is never easy, regardless of the trait.

In the Cole *et al.* [1] work, it took the measuring of problem solving in over 400 birds, taken briefly into captivity, followed by the counting of the number of eggs laid by those birds over the four years, to show an effect. Although it is standard procedure to test cognitive abilities in birds over the course of hundreds or thousands of trials, it is far from standard to examine those abilities in over 400 birds. Testing of subjects may also occur across years, especially in long-lived species like corvids, pigeons or primates [2], but never with such a number of subjects and not associated with offspring production or success.

Cole *et al.*'s [1] pioneering work will not be easily augmented. This is not least because in the great tits, the authors could couple two major logistic advantages: access to a large number of subjects, close to hand, from the well-known breeding population in Wytham Wood plus the great tit temperament. These birds respond well enough to captivity to allow experimental behavioural manipulations in a period of time short enough to enable the testing of many animals [3]. As ever, success lies in the logistical features

of a system and the testing of cognitive abilities in wild animals is heavily reliant on combining the right animal with the appropriate testing conditions. To date, there are few systems where cognition in wild animals has been examined in depth and most of these depend, as in Cole *et al.*'s [1] work, on tests of cognitive performance in animals in captivity [4–7], although there are exceptions, such as the testing of a range of cognitive abilities in hummingbirds [8–11], of spatial abilities in primates [12] and problem solving in New Caledonian crows [13,14].

That it will prove hard to follow the lead of Cole *et al.* [1] is a pity as their study is both timely and crucial. Timely because there is increasing interest in the role that cognition plays in decisions that animals make [15,16] and crucial because it is becoming clear that what constitutes cognitive ability depends, not on the eye of the beholder, but rather, on the mind of the experimenter. In Cole *et al.* [1] (and in an earlier paper [17]) the measure of cognitive ability is based on the ability of the great tits to solve a problem, which was to remove a lever from a device in order to gain food. Problem solving, although often regarded as requiring some cognitive skill, is actually a rather difficult ability to measure objectively. Typically the problem is one that is set by an experimenter, who by designing an experiment necessarily imposes a subjective degree of difficulty on the 'problem'. Such problems often require an animal to manipulate a component of a piece of equipment to access food (as in Cole *et al.*'s [1] work). Classic examples include Köhler's chimpanzees that pushed and stacked boxes to obtain food [18] and wild blue tits became the bird brains of Britain by solving a garden version of a task similar to that used by Cole *et al.* [1]. More recently though, Betty the crow bent a piece of wire into a hook to access food that was out of reach [19], and indeed, corvids have now eclipsed blue tits in the bird-brain stakes because they can solve what seem to be harder problems.

There is a problem, however, with using problem solving as a measure of cognitive ability. Firstly, what constitutes a 'problem'? It might seem clear that since animals face problems every day in obtaining food, food-finding or obtaining food tasks represent 'real' problems for animals, but do they? We only assume that manipulating moveable parts of a device containing food (or bending wire) is analogous to natural foraging. Second, and more importantly, how do we rate the difficulty of a problem? Is it the number of steps the animal must complete before success, or the number of different physical manoeuvres required for success? If so, this risks us imposing our idea that complex is the same as 'hard' (and what if each step is easy?). Or should we use the performance of the animals, such as the time taken to solve the problem, or the number of attempts that are successful? When performance is measured like this, there is the well-known confounding effect of motivation. If an animal does poorly, is it because the task is hard, or because they are stressed by the testing conditions (which may or not be due to task difficulty)? Furthermore, do we want tasks where success or failure is the only possible outcome (as in Cole *et al.* [1])? These designs may lack sensitivity to resolve variation among individuals and we very rarely assess our own performance dichotomously, and neither does natural selection. We do believe that problem solving is telling us something about cognitive ability but the problem we have yet to solve is quite what that something is.

There is one final reason why it has taken so long to demonstrate the fitness benefits of superior cognitive abilities: as with everything in evolution, being smart doesn't come for free. Great tits that solved Cole *et al.*'s [1] foraging problem laid more eggs and fed their babies less often but they were also more likely to desert their nest, for reasons as yet unclear. They are also less competitive at feeders than nonsolvers [17]. One possible explanation is that the problem solvers are more susceptible to stress [20], but why this would be so is also unclear.

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