EDITORIAL

Animal Cognition

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This special issue of *Integrative Zoology* (the official journal of the International Society of Zoological Sciences and the Institute of Zoology, Chinese Academy of Sciences) is focused on questions concerning the cognitive abilities of animals. The papers in this issue are the outcome of the 9th International Symposium of Integrative Zoology from 27-31 August 2017 in Xining, Qinghai Province, China. Each of these papers showcase questions absorbing the current interest of researchers in animal cognition (Healy 2019). Those questions range from the methodological through experimental design to the relationship between cognitive abilities and their neural underpinnings, from the laboratory to the field, and to the very nature of cognition. Furthermore, elegant experimental design has long been the hallmark of work on animal cognition (many examples in Shettleworth 2010) and this Special Issue contains several new instances.

For several decades prior to the current enthusiasm for using corvids and their close relatives to investigate cognitive abilities such as causal reasoning and social inferences, species such as Clark's nutcracker *Nucifraga columbiana* played a significant role in animal cognition through the analysis of the memory capabilities associated with food storing and spatial memory. These birds continue to be a useful workhorse for questions concerning spatial information processing where the particular question for Kelly *et al.* (this volume) is how these prodigious food storers (storing many thousands of food items each autumn) achieve the extraordinary accuracy with which they search for their caches. This is especially apparent as the visual appearance of the local environment during retrieval when all the leaves have fallen from the trees and the ground is densely covered in snow is changed to a considerable degree from that during caching in the autumn. Previous work had shown that when retrieving caches in the laboratory, nutcrackers used multiple visual

landmarks rather than beaconing to hidden caches using a single landmark. The question for Kelly *et al.* (2019) was whether the use of multiple landmarks could help wild birds to reduce error introduced to their search when using the sun compass to navigate to hidden caches: although the sun may be an effective tool for determining direction over many kilometres, it may not allow for sufficient precision when retrieving caches. Kelly *et al.*'s test was to clockshift nutcrackers searching for their caches in an outdoor aviary in the presence of one, or four, landmarks. Because a single landmark provides only one distance and direction to a cache, they suggested that searching in the presence of just one landmark would be much more susceptible to manipulations of the sun compass (achieved by clock shifting the birds) than if caching and searching are undertaken in the presence of multiple landmarks. Multiple landmarks, on the other hand, provide various ways to encode cache locations including angles between landmarks search is less susceptible to compass errors. And, indeed, Kelly *et al.* found no effect of clockshifting on the nutcrackers searching in the presence of four landmarks but when clockshifted by two hours the search error was more than twice as great than it was in birds not clockshifted. The combination of clockshifting in a setting where search accuracy can be measured allows tests of navigational hypotheses that are problematic with species that do not store food where one is reliant either on a lengthy period of training or on testing in the field where cue manipulations and measurement of search accuracy are next to impossible.

Rufous hummingbirds *Selasphorus rufus* provide a rare case where both are possible and Tello Ramos *et al.*'s (this volume) experiment in the latest in a multi-decade series of experiments investigating spatial memory in wild birds. The question for Tello Ramos *et al.* (2019) was also one of how animals might combine multiple sources of information to relocate rewarding locations. In this case,

however, the question was whether the birds use temporal information alongside spatial information to return to flowers because spatial information alone is insufficient when flowers take time to replenish their nectar supplies: a bird that returns too soon may find the flower not yet replenished, while a bird that returns too late may find that a competitor has already drunk the flower's contents. While a bird might remember each and every flower it visits, a hummingbird's cognitive load might be diminished if he remembered a route around his flowers and associated that with a regular temporal duration. While birds in Tello Ramos *et al.*'s experiment did repeat the order in which they visited patches of flowers and increasingly at the appropriate interval, when they visited patches of flowers too soon, they avoided visiting the flowers in that patch that they had emptied on the previous bout. They appear, in fact, to have remembered their visits to each flower before they learned to time their visits to each patch so as not to have to remember each flower. This better than necessary performance in this task reminds us to take care with assumptions of the relationship between cognitive capacities and brain size: rufous hummingbirds have a brain somewhere between the size of a grain of rice and a baked bean.

Brains are very much on the minds of Sherry & Guigeno (this volume) who, like Kelly *et al.* (2019), investigate the neural basis of spatial information processing in a species known for its dependence on spatial memory: the female brown-headed cowbird *Molothrus ater*. She is a brood parasite that searches for host nests and returns to lay her eggs in these host nests when they are at a suitable stage (containing at least one host egg). Her mate very much leaves her to it. Sherry & Guigeno (2019) found that female brown-headed cowbirds outperformed conspecific males on one spatial task but not another and that females had greater hippocampal neurogenesis than did males, a sex difference not seen in red-winged blackbirds *Agelaius*

phoeniceus, a closely related species that is not a brood parasite. An association between neural data and performance on one apparently spatial task but on not another causes us to examine more closely what ability the animal might actually use to perform well in tests we assume assess a particular cognitive ability (for Sherry & Guigeno, spatial memory). In the Sherry & Guigeno case, it is possible that the task (memory for location a of rewarded cup in an enclosure) in which the females outperformed the males was more similar in its cognitive demands than the other (a delayed matching to sample task presented on a touchscreen). But this is an after the fact interpretation, which, as the authors say, needs testing.

The value of designing the appropriate experiment is shown by Subias *et al.* (this volume) who provide both a new species for testing cognitive abilities in animals (red-tailed black cockatoos *Calyptorhynchus banksii*) and a method for testing reasoning in animals. Unlike tests for spatial learning and memory in animals, which have a long and rich history, demonstrating that animals solve a problem by inferential reasoning is not straightforward. The demonstration, for example, of transitive inference (i.e. knowing that if A<B<C then A<C), does not confirm that the animal understands the relationship between the items in the sequence. Indeed, the large number of species that seem to behave as if they can derive such relationships may have encouraged closer focus on possible alternative explanations. Whatever the explanation for transitive inference, evidence for another form of reasoning, gathering support for reasoning by exclusion (where the subject has to infer which is the correct choice by inferring that the correct choice is the one for which they have no information e.g. show an animal a cup that does not contain food and it should choose the other cup because the animal 'understands' that the other cup must then contain food) has been much more difficult. One explanation might be that this form of reasoning is relatively rare and has not

evolved in most birds while another is that the tests have not been appropriate: failure on a task has multiple explanations other than that the animal lacks the ability to solve the task. Until an animal solves a task, then, it is extraordinarily difficult to examine alternative explanations. Therefore, as the data on red-tailed black cockatoos that Subias *et al.* present are at least consistent with the interpretation that these birds are capable of reasoning by exclusion, this species gets over the first hurdle in the testing for this capacity and is available for tests of possible alternative explanations. Although parrots and corvids are currently the favoured avian species for such tests, they are helping to produce increasingly robust methodologies that will provide useful for testing reasoning by exclusion in a wider taxonomic range.

Not only is the development of new experimental paradigms important for increasing the taxonomic range of species available for cognitive investigations, so is the development of appropriate technologies. Video recording is one very familiar method used to quantify behavioural responses in many different species. As screen refresh rates have increased so has the capacity to present subjects with video stimuli to which subjects respond with natural behaviours. The question that Guillette and Healy address in this volume is whether the behaviour(s) elicited are similar in degree as well as kind as if the subject was responding to a live animal. If this were to be the case, video presentations could revolutionize tests of animal cognition by reducing the number of animals used in experimental tests, enabling experimental manipulations that are not possible with real animals, increasing standardization of stimuli and more. And, indeed, as propensity for male zebra finches to copy material choices of demonstrators they saw on a video was qualitatively similar to the degree to which observers copied material choices of live birds (Guillette & Healy 2019), video presentations may be useful in the social learning experiments. But as there was a

substantial quantitative decrease in the effect of observation for the birds watching demonstrators via video relative to those birds watching live demonstrators, the increase in sample size required to achieve significance may counter some of the benefits of using video presentations.

Although Frohnweiser *et al*. (this volume) are also developing methodology for presenting stimuli to experimental subjects, theirs is a more recent technology than video: they are interested in the use of robotic animals for eliciting natural, or at least meaningful, responses in subjects. Unlike video presentations where the observers appear at least to pay attention to conspecifics or heterospecifics, albeit perhaps not to the same extent as they would to live animals, with robotic animals, the question is what features are required in robotic animals such that they are perceived appropriately. Using bearded dragons *Pogona vitticeps* Frohnweiser *et al.* (2019) found that males used their left eye more to look at a motionless robot (a 3D printed model of a bearded dragon with an articulated head) than when they looked at a robot dragon bobbing its head. Females, on the other hand, did not differ in which eye they used, irrespective of movement. Neither the colour of the robot nor the presence/absence of eyes affected the way in which male or female bearded dragons looked at the robots. These data suggest that movement is especially relevant but much more so to males. Given that both male and female bearded dragons use and respond to head bobbing in dominance displays, the lack of response from females suggest that the model used by Frohnweiser *et al.* did not capture sufficient features of a real bearded dragon to elicit a response. As head bobbing is more common in males than it is in females, however, this variation in the strength of responses to head bobbing may indicate that Frohnweiser *et al*. have actually captured to a feature appropriate for incorporation into a robotic bearded dragon.

And finally, Kriengwatana (this volume) gets to grips with a fundamental issue facing workers in animal cognition: how and whether different cognitive processes or abilities are related to each other. In particular, she discusses the possible relationship between bird song, which is learned, and other cognitive abilities such as spatial memory, both of which are negatively affected by poor conditions during development. As the evidence for a close relationship among cognitive abilities is, perhaps surprisingly, far from strong, Kriengwatana (2019) suggests that it might be useful to focus first on abilities that are plausibly functionally related such as song learning and social learning.

Examining correlations among cognitive abilities is, undoubtedly, going to be a feature of animal cognition in the coming decade(s). Although it is common to consider brain size as a measure of cognitive ability, the current lack of correlations between performances on differing cognitive tests would suggest otherwise. Or perhaps the problem lies with the nature of the tests we use: can we be sure that our tests do reveal the cognitive abilities we think they do? Common to all the papers in this volume is the issue of getting the experimental design 'right' and ensuring that the ability assumed to be under test is the one the animal uses to solve the problem. No matter how sophisticated our technology becomes, this remains the key to making advances in understanding animal cognition.

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