Preface

Comparative cognition: Function and mechanism in lab and field. A tribute to the contributions of Alex Kacelnik

At the 2011 meeting of the International Society for Comparative Cognition in Melbourne, FLA, Alex Kacelnik received the Society's Research Award, presented annually since 2002 to an individual who, throughout his or her career, has made "outstanding contributions to the study of cognitive processes in animals." Alex was therefore the tenth recipient of the award. He was also the first not based in North America and not primarily in a Department of Psychology: Alex is Professor of Behavioural Ecology in the Department of Zoology at Oxford University, where he has done much of his work. These distinctions say much not only about Alex's accomplishments, but also about the growth and maturation of the field and the Society.

The occasion of the award is usually marked by, among other events, a symposium of talks by the awardee's past and present students and colleagues. Articles by the presenters and others similarly associated with Alex over the years form the Special Issue of Behavioural Processes from which you are now reading. There could not be a better introduction to Alex's work and influence than this collection of articles. Those who know him primarily as the father of Betty the Crow, from the recent highly publicized work of his group with the tool-using New Caledonian crows (e.g. Weir et al., 2002), will see that the cognition underlying tool use is just one of the newest interests in a wide-ranging career.

Alex began his academic training in Buenos Aires, Argentina, in physiology and pharmacology, but moved to Oxford in the mid 1970s to work with David McFarland and John Krebs, completing his PhD with Krebs in 1979. Experimental tests of optimal foraging theory were just getting off the ground in the early 1970s. One of the most influential examples of this direction in the new field of behavioral ecology was Krebs, Kacelnik, and Taylor's (1978) *Nature* paper on optimal sampling by great tits. The article reports the behavior of these small wild birds in a laboratory "two-armed bandit" task designed to test a model of optimal sampling during learning. In effect, it modeled the optimal way to learn which is the more frequently rewarded option in a probabilistically rewarded choice situation. As can be seen in the contribution to this Special Issue by Lea and colleagues, this article is still influential. And as can be seen in many of the other contributions as well, it struck an important theme in Alex's work, that of careful behavioral tests closely tied to quantitative modeling.

After completing his PhD, Alex held a series of research positions, in Oxford, in Groningen, the Netherlands, and at King's College Cambridge, eventually returning to Oxford as a Lecturer and now Professor in the Department of Zoology. One of my oldest memories of Alex is from when, during a visit to Oxford, I was taken out to the University Farm (now the John Krebs Field Station), where in one of the buildings Alex had starlings performing in operant experiments. These were very much in the spirit of the Krebs, Kacelnik, and Taylor study, now looking at the roles of travel time and reward size in choice in a situation designed to capture a real-world foraging problem. And out of the window one could see what it was. Starlings were raising their young in nest boxes set up around the farm buildings, and somewhere in a nearby field there was a little tent, a canvas hide, with a shivering graduate student inside dispensing mealworms down a pipe for starlings arriving outside to collect and carry home to their nestlings. Again the goal was to test the predictions of a model of ecologically relevant behavior – here how many mealworms the birds collected to carry back to the nest (load size) as a function of travel time, or distance of the tent "patch" from the nest, a technique Alex developed while in Groningen (see Kacelnik, 1984). The approach was absolutely classic in combining observations and experiments in the field, in the great Oxford tradition exemplified by Niko Tinbergen, with laboratory experiments, always closely tied to rigorously formulated theory.

The starling work led on to a very fruitful collaboration on timing with John Gibbon, thus bringing into the picture the psychology of decision-making and situating Alex's work firmly in the mainstream of comparative cognition. This collaboration resulted in a landmark *Psych Review* paper by Gibbon, Church, Fairhurst and Kacelnik (Gibbon et al., 1988) and in the use of scalar timing theory by Alex and a series of students to understand decision-making under risk (Kacelnik and Bateson, 1996; Kacelnik and Todd, 1992). Ultimately the further and deeper development of this same integrative approach led to testing ideas about economic decisions. The relationships among economics, foraging, and the psychology of decision-making is beautifully explicated in Alex's chapter (Kacelnik, 2006) comparing biological, psychological, and economic approaches to rationality. Work continuing this integration is still ongoing in Alex's lab, as can be seen in the article by Aw et al. in this issue.

The Comparative Cognition Society was not the first, nor the last, to honor Alex's contributions. His other awards include the award of the Swiss Cogito Prize in 2004, shared with experimental economist Ernst Fehr, and in 2009 a prize for lifelong contributions from the Argentinian Society for Neuroscience. Most recently, he was elected to the Royal Society of London, the ultimate accolade for British scientists.

The first half of this Special Issue consists of articles on the general theme of connecting functional models of foraging with...
psychological mechanisms of reinforcement, timing, and decision-making, wherever possible integrating laboratory analyses with insights from the field. As he did in the symposium in Melbourne, Stephen Lea and colleagues kick off by updating the models of learning on a “two-armed bandit”, comparing the type of model used originally by Krebs et al. (1978) to other approaches, and to more recent data. The continuing fruitfulness of Krebs, Kacelnik, and Taylor’s work is likewise illustrated in the article by Dunlap and Stephens reporting experiments with blue jays on the role of memory in tracking changing environments.

The next five articles all address different kinds of foraging decisions in a known, stable, environment with options differing in delay and/or amount of reward or – in the case studied by Healy and colleagues with hummingbirds in their article – in the overall context of other available rewards. The first two of these, by Aw et al. and by Shapiro et al., both with Alex as senior author, illustrate the depth and scope of the research on decision-making under risk that has developed in Alex’s lab. They also illustrate the elegance of the operant experiments with starlings (little black Oxford pigeons) that have evolved since the long-ago days at the University Farm.

The way in which animals, including people, respond to delayed rewards has long been of interest in contexts other than foraging, particularly in the comparative study of “self-control” or “patience”. The hypothesis that life history variables predict a species’ willingness to wait for a large delayed reward is addressed in the study reported by Stevens and Mühlhoff with three species of lemurs, animals not previously tested in self-control paradigms. The importance of other factors in determining optimal choice in such paradigms is examined in the concluding article of this group, the modeling paper by Fawcett et al., in which the authors suggest new directions for the comparative study of patience.

The next two articles, by Tuero, Fiorini, and Reboreda and by Fernandez-Juricic, continue the theme of integrating function and mechanism, here with respect to aspects of avian behavior. Alex has long collaborated with Juan Reboreda on the nest-parasitic behavior of Argentinian cowbird species (e.g. Reboreda et al., 1996). The cowbirds are represented here in the study combining data from the field with that from an experiment on captive birds to address a theoretical prediction about when cowbirds should eliminate potential competitors for their future offspring by pecking holes in the eggs already in a nest they are parasitizing. Alex’s former student Esteban Fernandez-Juricic likewise reports on the latest developments in work begun with Alex (see Fernandez-Juricic et al., 2004) involving how the features of a bird’s visual system including field of view and type of fovea should – and do – influence its vigilance behavior.

The recent interest of Alex’s group in the study of birds’ tool use and its cognitive underpinnings is represented by the next two articles, by Rutz and St Clair and by Tebbich and colleagues. At the symposium in Melbourne, Christian Rutz entertained and enlightened us with preys’-eye views of New Caledonian crows using tools in the field. In their article, he and St Clair summarize the latest information about the natural context of tool use by these animals and use it to base speculation about how and why they might have evolved tool use. Evolution and function of avian tool use is also the context in which Tebbich and her colleagues report new observations on their study species, the Galapagos woodpecker finch, the only other bird known to customarily use tools.

The last three articles in this Special issue take the integrative approach exemplified by Alex’s work beyond foraging to other ecologically important problems. Houston and colleagues apply optimality modeling to the general issue of “optimism”, asking whether animals should ever behave as if the world is better than it is or if they only appear to. Chappell and colleagues address the same general issue addressed by Krebs et al. (1978), how best to gather information in a novel situation, but in the broader context of how to design artificial as well as natural systems. And finally, Brunner and colleagues take us to the real world of neurological disease in their illuminating discussion of how research in comparative cognition can contribute to drug discovery.

Similar to a poster presented to Alex by his lab at the celebrations in Melbourne, the word cloud on the cover represents the relative frequencies of words and terms in the titles of Alex’s publications. It was created by Associate Editor Marco Vasconcelos, together with Tiago Monteiro. Although the obvious suspects of foraging, starlings, tool use and New Caledonian crows loom largest, along with terms such as decision making, patch, and models, the sharp-eyed reader can also find toads, guinea pigs, lizards, and honeybees, as well as evidence of Alex’s ventures into the brain in mesencephalic and hippocampus.

Marco and I thank all the authors for their contributions to this Special Issue. Some of them assisted in reviewing manuscripts, as did Robert Gerlai, and we are grateful for this help. Finally, I thank Marco Vasconcelos for his work as Associate Editor, for both handling some of the manuscripts and providing advice and support throughout. To someone who has never edited a volume before, the Comparative Cognition Society’s invitation to edit an issue honoring Alex at first seemed a daunting and not entirely welcome task. It has been a pleasure to see how – thanks in large part to the contributors’ enthusiasm – it has come together in such a wide-ranging tribute to his influence.

References


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