



## Forum Article

## On problem solving and the evolution of cognitive abilities by mate choice: a reply to Camacho-Alpízar et al. (2020)

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In an earlier study (Chen et al., 2019, *Science*, 363(6423), 166–167), we showed that budgerigar, *Melopsittacus undulatus*, females increase their preference for males that were observed solving two extractive foraging problems. Camacho-Alpízar et al. (2020, *Animal Behaviour*, 165, e1–e3) question whether this outcome shows that females evaluate the cognitive skills of males. Their main argument is that individual differences in problem solving are often due to differences in noncognitive abilities. Here we outline the differences between the use of problem-solving tasks as it is mostly done and how we used it in our study. We argue that our design maximizes the chance that observed differences in male problem solving indicate differences in learning abilities to an observing female. We agree with Camacho-Alpízar et al. that the topic of the evolution of cognitive abilities through sexual selection deserves further study and hope our study (Chen et al., 2019), Camacho-Alpízar et al.'s comment and this reply will stimulate further research.

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Camacho-Alpízar et al. (2020, this issue) comment on our study (Chen, Zou, Sun, & ten Cate, 2019) showing that female budgerigars, *Melopsittacus undulatus*, increased their preference for males that they observed solving two different extractive foraging problems. They do not contest the result, but question whether the result should be interpreted as indication that females evaluate cognitive skills of males. The core of their argument is that variation in problem solving need not depend on cognitive abilities and hence that variation in successful solving need not indicate variation in cognitive abilities. However, the way in which we use the task differs in several important respects from how it is used in most studies. We therefore question the relevance of their comments for the interpretation of our study. Nevertheless we welcome their commentary, as we agree that using a problem-solving task to measure cognitive performance is not without complications and a discussion of the issue is therefore relevant and useful.

Below we first briefly indicate the background and aims of our study. Next we outline the differences between the use of problem-

solving tasks as it is mostly done and how we used it in our study. We discuss whether this affects any inferences it allows about cognitive abilities. We also give attention as to why budgerigars are an excellent model species to examine the topic.

## WHAT DRIVES THE EVOLUTION OF COGNITIVE TRAITS?

It is widely accepted that cognitive abilities can vary both within and between species. The evolutionary causes and consequences of this variation are still debated, but there is some consensus that between species more complex cognitive skills correlate with certain conditions such as living in a variable or unpredictable habitat, extended longevity, omnivorous diet, high sociality and a large relative brain size (e.g. Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005; Emery, 2006; Overington, Morand-Ferron, Boogert, & Lefebvre, 2009; Reader, Morand-Ferron, & Flynn, 2016). These characteristics are present in mammal species like humans and apes, but also some corvids and parrots, which are acknowledged as showing more complex or flexible cognitive abilities than other avian taxa (Emery & Clayton, 2004; Emery, 2016; Lambert, Jacobs, Osvath, & von Bayern, 2019). The ecology and life history of budgerigars show many of the characteristics mentioned above: they are highly social and long-lived, they live in unpredictable and

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highly variable habitat (Kaplan, 2015; Wyndham, 1980) and they have a large relative brain size, even for a parrot species (Franklin, Garnett, Luck, Gutierrez-Ibanez, & Iwaniuk, 2014). Budgerigars also show evidence of excelling in some cognitive domains. For instance, when trained to discriminate two sets of auditory sequences organized according to different rules, they were capable of correctly classifying novel sequences conforming to one or the other rule. This ability for rule abstraction was not present in a songbird, the zebra finch, *Taeniopygia guttata*, tested in the same way (Spierings & ten Cate, 2016). These characteristics make budgerigars a promising species to address the factors that may contribute to the evolution of cognitive traits.

In our study (Chen et al., 2019), we focused on whether sexual selection may be driving cognitive skills involved in solving an extractive foraging problem. If solving such problems is dependent on cognitive skills (which we discuss below), then the question arises which selective forces may affect the evolution of such skills. One might be natural selection: birds capable of skilled food extraction may survive better or be in better condition, which may translate into higher fitness. Another selective force might be sexual selection: a preference for mates capable of skilled food extraction might benefit the choosing partner as it may get a mate better able to forage and access food for offspring and/or it may get offspring with better cognitive abilities. For budgerigars, in which females depend on male food provisioning during breeding and right after hatching (e.g. Stamps, Clark, Arrowood, & Kus, 1985), this ability may be quite relevant. However, how can a female assess the solving skills of a potential partner? There is some evidence from other species that cognitive traits may be correlated with some behavioural or morphological phenotype. For instance, the blue-black crown coloration in great tits, *Parus major*, correlates with problem solving and learning performance (Cauchard, Doucet, Boogert, Angers, & Doligez, 2017), which may then become the target for selection. However, the link between coloration (or, more generally, any other morphological or behavioural trait) and cognition may be neither direct nor strong. Another possibility for sexual selection to operate on cognitive traits would be if individuals select their mates based on observing their cognitive skills directly (Boogert, Fawcett, & Lefebvre, 2011). In our experiment we tested this idea by creating a contrast between two potential partners: one that was observed to open two types of problem boxes and one that was unable to open the boxes.

## RELATING PROBLEM SOLVING TO COGNITIVE ABILITIES

As outlined by Camacho-Alpizar et al., the relation between problem solving and cognition is not as obvious as it may seem at first sight. Studies of both inter- and intraspecific variation in problem solving have indicated that this variation can often be attributed to differences in noncognitive factors like neophobia, motivation, exploration, motor diversity and/or persistence in the task (e.g. Griffin & Guez, 2016). This is also supported by a modelling study in which Guez and Griffin (2016) showed that noncognitive factors like persistence and motor flexibility can explain observed variation in innovative problem solving. Note, however, that most of these studies used a relatively simple, single-step task, such as lifting the lid of a Petri dish or pushing a barrier to the side. Success in problem solving is mostly measured as the latency or number of attempts or trials needed to solve the problem *for the first time* (Guez & Griffin, 2016, p. 1450). Guez and Griffin also emphasized that their models apply to solving a single-step innovative foraging problem for the first time and added that 'it is rarely in the first occurrence of a behavior that one should seek an involvement of cognition' (Guez & Griffin, 2016, p. 1459). We agree. However, cognitive factors can come into play if one presents a problem-

solving task repeatedly, as this opens the scope for learning, a cognitive trait. In line with this, several studies (e.g. Benson-Amram; Holecamp, 2012; Huebner, Fichtel, & Kappeler, 2018; Overington; Cauchard; Côté, & Lefebvre, 2011) have used or suggested using (e.g. Morand-Ferron, Cole, & Quinn, 2016) variation in performance on successively solving a problem as an indicator of variation in learning ability.

## RELATING PROBLEM SOLVING TO LEARNING

If the first instance of solving a problem is not closely related to cognitive abilities of a solver, but improved performance over time is, then individuals seeking a mate might be sensitive to indications of better learning/cognitive abilities. Such an indication might be that a potential partner solves a sequential multistep extractive foraging problem without extensive exploration and repeated trying. This may indicate to an observer that the partner has learned the task (by operant and sequential learning) or even may have some insight into the problem or a physical understanding of it. Another indication might be whether the other individual is capable of solving several different extractive foraging problems. In our experiment we tried to create a condition in which females would have the opportunity to observe two males showing a maximum contrast in skills, from which females might potentially infer each male's learning capabilities. One male was, through training, skilled in two tasks: opening of a Petri dish and opening a problem box requiring the sequential performance of three acts: lifting a lid, opening a door and pulling a drawer. The other male was unable to open these boxes because he was not trained to do so. Over a series of six observation days the females observed the skilled males opening the boxes. Each problem was presented several times on 3 days. The control males, which were observed equally often by the females, were familiar with the boxes and showed no indications of neophobia. Some repeatedly tried opening the boxes, but they never succeeded. In this way, we tried to maximize the chances that females might perceive the difference between the males as being due to learning or some other cognitive quality. Relevant in this context is also that budgerigars that observe a demonstrator obtaining food by a specific way of opening a food box (Mottley & Heyes, 2003) or by performing another type of operant behaviour to get access to food (Mui, Haselgrove, Pearce, & Heyes, 2008) tend to imitate the behaviour of the demonstrator. So, budgerigars do not just attend to the outcome (access to food) of a behaviour, but also to the way in which it is obtained. This is also supported by one of our control experiments, in which females were exposed to the contrast between a male having access to food without the need to perform any opening behaviour and a male having no access to food. In this experiment the females did not increase their interest in the male with food access. Both our control experiment and the experiments showing imitation of a demonstrator make the suggestion by Camacho-Alpizar et al. (2020) that females are more interested in 'food producing' rather than problem-solving males less likely.

## CONCLUSION

We acknowledge that it is hard to fully exclude that females attended to some behavioural feature of males that was correlated with, but causally unrelated to, learning or some other cognitive skill involved in problem solving. We therefore agree with Camacho-Alpizar et al.'s suggestion for follow-up experiments. Such experiments may address the presence of interindividual variation in spontaneous male problem-solving abilities and subsequent improvement by learning, or whether females that observed the opening behaviour are more likely to use it themselves later on.

Additionally, it will be useful to develop other types of tasks that can reveal cognitive skills to observers, while studies in other species may test our suggestion (Chen et al., 2019) that a sensitivity to learning skills of a potential partner might be expected, in particular, in species showing social learning and imitative behaviour. Finally, we did not claim or want to claim that learning to solve extractive foraging problems is indicative of an individual's cognitive abilities in other domains, such as the rule abstraction mentioned above (Spierings & ten Cate, 2016), or reflects some general cognition 'g' (Burkart, Schubiger, & van Schaik, 2017; Boogert, Madden, Morand-Ferron, & Thornton, 2018). However, we do consider it worthwhile to examine whether cognitive abilities in food extraction tasks correlate with cognitive abilities to solve tasks in other domains (e.g. Medina-García, Jawor, & Wright, 2017). We thus hope that our study, as well as the commentary by Camacho-Alpizar et al. (2020) and this reply, may stimulate researchers to put various hypotheses to the test as well as to design further experiments which may reveal cognitive differences to potential partners.

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