**Are cognitive abilities under selection by female choice?**

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**Summary**

A recent paper by Chen et al. 2019 found that female budgerigars (*Melopsittacus undulatus*) show a preference for males that are successful problem solvers. Is this result sufficient to conclude that mate choice influences the evolution of cognitive abilities? Here, we consider what we currently know about the relationship between problem-solving and cognition. We argue that it is premature to conclude, based on these findings, that cognitive abilities have evolved in part through sexual selection by female choice.

**Keywords**

Cognitive evolution, Mate choice, Problem-solving, Sexual selection

**Introduction**

 Is cognition under sexual selection? In a recent paper by Chen and collaborators (2019), female budgerigars (*Melopsittacus undulatus*) altered their mate preference to an initially less-preferred male after observing that less-preferred male successfully solving and obtaining food in an extractive foraging task. In contrast, in control trials where females observed the initially less-preferred male eating from a regular food container, female birds did not shift their initial male preference. A new group of females given the opportunity to watch females, rather than males, problem-solve did not prefer problem-solving females over non-solvers. The authors draw upon this pattern of findings to conclude that female budgerigars select males based on an evaluation of their problem-solving abilities, in line with the hypothesis that cognition is under sexual selection. We consider this interpretation troublesome.

Chen et al.’s conclusion relies firstly upon the assumption that successful problem solving is indicative of superior cognitive abilities compared to non-solving, and second, that problem solvers use cognition to solve extractive foraging tasks, that is, that problem-solving employs, or is *per se*, a cognitive ability. Yet neither of these assumptions might be true (Griffin & Guez, 2014, 2016). We consider each of these assumptions, separately, below.

Although the term cognition is a nebulous concept and the widely employed definition is broad (see Shettleworth, 2010), the animal cognition literature generally agrees that learning (e.g. associative learning, discrimination learning, reversal learning, etc.) is a cognitive ability while processes such as motivation, persistence, neophobia and motor diversity are not (Griffin, Guillette, & Healy, 2015; Rowe & Healy, 2014; Shettleworth, 2010; but see Greggor, Thornton, & Clayton, 2015; Griffin, Netto, & Peneaux, 2017 for alternative viewpoints on neophobia/neophilia). Many experiments measure cognitive performance by quantifying the number of errors, the number of trials, or the total time to reach a pre-defined level of performance on a given test after controlling for other ‘noncognitive’ factors (Huebner, Fichtel, & Kappeler, 2018; Langley, van Horik, Whiteside, & Madden, 2018; van Horik & Madden, 2016). Here, our point is not to discuss the validity of such operationalization of cognitive performance, but only to examine the conclusions of Chen and collaborators against this background of accepted methodologies. While Chen et al. do not themselves specify what they mean by their repeated use of the term cognitive abilities/skills, their mention of noncognitive processes suggests they endorse this heuristic.

**Is variation in problem-solving success indicative of variation in cognitive ability?**

 There is currently very little empirical evidence to support the assumption that inter-individual variation in problem-solving performance is indicative of inter-individual variation in general cognition. To date, only one study has compared species’ performances on both a problem-solving task and a learning task and found no relationship (Tebbich, Stereln, & Teschke, 2010). Although woodpecker finches (*Camarhynchus pallidus*) outperformed tree finches (*C. parvulus*) on an extractive foraging task (i.e., problem solving), woodpecker finches did not learn a colour discrimination task in fewer trials (Tebbich et al., 2010). Equally, multiple intra-specific studies in birds and mammals have repeatedly failed to find any evidence of positive correlations between inter-individual variation in problem-solving success and inter-individual variation in learning performance (e.g., spatial learning in grey mouse lemurs *Microcebus murinus*, Huebner, Fichtel, & Kappeler, 2018; associative learning in pheasants *Phasianus colichus*, van Horik & Madden, 2016). Furthermore, in other research comparing problem-solving to multiple measures of learning, problem solving correlates positively with initial discrimination learning but inversely with reversal learning (e.g., common mynas *Acridotheres tristis*, Griffin, Guez, Lermite, & Patience, 2013). The lack of consistently positive relationships between problem solving and learning challenges the assumption that problem-solving performance is indicative of a species’ or an individual’s general cognitive abilities. This caveat in turn challenges any conclusion that selection of problem-solving males by females provides evidence that inter-individual variation in cognition is under sexual selection.

**Is problem solving a cognitive ability?**

 There is now a strong body of empirical evidence that individual variation in problem-solving performance can be determined by multiple behaviours unrelated to what is considered by main-stream cognitive scientists to be part of cognition. Any one of these behaviours could form the basis of a female’s preference for a successful problem-solving male. Non-cognitive behaviours known to influence problem solving performance and relevant to our argument include neophobia, exploration, persistence, motor diversity, and age, to which one should add all potential interactions between these behaviours, about which much less is known (see Griffin & Guez, 2014). We briefly describe what is known about the influence of each of these variables on problem-solving (for reviews and more in depth analyses, see Griffin & Guez 2014; 2016)

While lower levels of neophobia (i.e. fear of novelty; Greenberg & Mettke-Hofmann, 2001) was originally proposed to facilitate problem solving, the effect of this behavior varies across species and context. For example, hyenas (*Crocuta crocuta*) that solved a puzzle box were less neophobic than hyenas that did not (Benson-Amram & Holekamp, 2012). In contrast, less neophobic meerkats are *less* likely to solve three different problem-solving tasks (Thornton & Samson, 2012). In common mynas, neophobia influences problem solving in some contexts (Sol, Griffin, & Bartomeus, 2012), but not others (Griffin, Diquelou, & Perea, 2014).

An individual’s propensity to explore is another variable whose influence on problem-solving appears to vary somewhat unpredictably. For example, in Carib grackles *Quiscalus lugubris*, successful problem solvers were more exploratory than non-problem solvers (Overington, Cauchard, Côté, & Lefebvre, 2011). In starlings, *Sturnus vulgaris*, however, exploratory behavior did not correlate with problem solving success (Boogert, Reader, Hoppitt, & Laland, 2008). While animal may acquire information by exploring their environment, it would be incorrect to assume that exploration always involves acquisition, storage and use of information. Moreover, the relationship between exploration and cognitive performance has been measured in multiple studies which have found the direction of that relationship to be highly variable (Dougherty & Guillette, 2018; Guillette, Hahn, Hoeschele, Przyslupski, & Sturdy, 2015; Guillette, Reddon, Hoeschele, & Sturdy, 2011).

But amongst the now large body of work on problem solving, by far the most robust predictors of problem solving is the persistence with which an individual interacts with a task and the diversity of the motor actions it deploys. The positive effect of persistence on problem solving success holds in pheasants, hyenas (Benson-Amram & Holekamp, 2012), meerkats (Thornton & Samson, 2012), great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) (Morand-Ferron, Cole, Rawles, & Quinn, 2011). Convergent evidence for the importance of persistence over learning has also been found in computational models of problem solving (Guez & Griffin, 2016). The positive effects of increased motor diversity in solving problems are found in common mynas (Griffin & Diquelou, 2015; Griffin et al., 2014), hyenas (Benson-Amram & Holekamp, 2012), and multiple urban birds (Diquelou, Griffin, & Sol, 2016)

 Age also influences problem-solving performance. In callitrichid monkeys (Callitrichidae), for example, juveniles were less likely to solve a task than adults (Kendal, Coe, & Laland, 2005). Such effects have also been reported in the system (budgerigars) used by Chen et al. (Medina-García, Jawor, & Wright, 2017). Higher exploration rate and lower juvenile neophobia were found to have a positive effect on problem solving performance (which Medina-García et al. measured as problem solving success combined with the number of trials before success). Overall, the literature on individual differences in problem solving performance shows more evidence for problem-solving success being influenced by non-cognitive factors than by cognitive abilities, casting additional doubt on the assumption that problem solving involves or is *per se* a cognitive skill.

 Despite our concerns with Chen et al. (2019) interpretation of their results, we applaud the approach taken to study female preference for males. The methodology provided a very clear result: males (but not females) become more attractive to female budgerigars after they have demonstrated successful problem solving. What then is it about successful problem-solving that attracts female attention and causes them to change their preference? We propose that females are being attracted to males that *produce* (rather than eat) food. Re-formulating ‘problem-solving males’ as ‘food-producing males’ makes it easier to realize that female choice likely operates on the behavioural outcome and not on the mechanism underpinning food production (e.g. cognition vs. persistence). For this reason, in light of the data reviewed above, inferring from Chen et al.’s findings that female selection acts upon male cognition is premature.

**Conclusion**

As Chen et al. (2019) mention in their paper, solving foraging problems might be advantageous and a desirable skill in a mate. However, evidence shows that success in problem solving is not necessarily predicted by cognitive abilities, and that inter-individual differences in problem solving performance are often influenced by aspects of behaviour typically considered by mainstream literature to be non-cognitive. Consequently, the results obtained by Chen et al. (2019) are not necessarily evidence that sexual selection affects the evolution of cognitive traits. In order to reach such a conclusion we consider it is necessary to demonstrate that the following conditions are met: (1) variation in problem solving correlates with variation in cognition (e.g. learning speed) in budgerigars; (2) there is natural variation in problem solving abilities among male budgerigars, (3) that individual male budgerigars are consistent in their problem solving abilities, and (4) that cognitive abilities in budgerigars are heritable (Boogert, Fawcett, & Lefebvre, 2011; Sorato, Zidar, Garnham, Wilson, & Løvlie, 2018). Further, convergent evidence that females act as selection agents for higher cognition in males requires demonstrating that (5) males outperform females on both problem solving and cognitive tests in budgerigars. Finally, we suggest a modification of Chen et al.’s elegant design would provide additional confidence that females select problem-solving males. In the experiment, females were given access to the problem-solving task for five minutes, after which they observed males solve the problem. This effort to solve the problem first might be critical to raising the females’ attraction to the successful males. However since no female was able to solve the problem, one cannot tell whether females’ own experience with the task influences her decision to shift choice of males. By allowing some females to solve the problem, one could ask whether females that solve the problem themselves also switch their preference to a problem-solving male. If females select food-producing males, then females should only select those males that produce food that females themselves cannot.

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**References**

Benson-Amram, S., & Holekamp, K. E. (2012). Innovative problem solving by wild spotted hyenas. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1744), 4087–4095. https://doi.org/10.1098/rspb.2012.1450

Boogert, N. J., Fawcett, T. W., & Lefebvre, L. (2011). Mate choice for cognitive traits: A review of the evidence in nonhuman vertebrates. *Behavioral Ecology*, *22*(3), 447–459. https://doi.org/10.1093/beheco/arq173

Boogert, N. J., Reader, S. M., Hoppitt, W., & Laland, K. N. (2008). The origin and spread of innovations in starlings. *Animal Behaviour*, *75*(4), 1509–1518. https://doi.org/10.1016/j.anbehav.2007.09.033

Chen, J., Zou, Y., Sun, Y. H., & Ten Cate, C. (2019). Problem-solving males become more attractive to female budgerigars. *Science*, *363*(6423), 166–167. https://doi.org/10.1126/science.aau8181

Diquelou, M. C., Griffin, A. S., & Sol, D. (2016). The role of motor diversity in foraging innovations: A cross-species comparison in urban birds. *Behavioral Ecology*, *27*(2), 584–591. https://doi.org/10.1093/beheco/arv190

Dougherty, L. R., & Guillette, L. M. (2018). Linking personality and cognition: a meta-analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756), 20170282. https://doi.org/10.1098/rstb.2017.0282

Greenberg, R., & Mettke-Hofmann, C. (2001). Ecological aspects of neophobia and neophilia in birds. In V. Nolan & C. F. Thompson (Eds.), *Current Ornithology, Volume 16* (16th ed., pp. 119–178). Boston, MA: Springer US. https://doi.org/10.1007/978-1-4615-1211-0\_3

Greggor, A. L., Thornton, A., & Clayton, N. S. (2015). Neophobia is not only avoidance: Improving neophobia tests by combining cognition and ecology. *Current Opinion in Behavioral Sciences*. https://doi.org/10.1016/j.cobeha.2015.10.007

Griffin, A. S., & Diquelou, M. C. (2015). Innovative problem solving in birds: A cross-species comparison of two highly successful passerines. *Animal Behaviour*, *100*, 84–94. https://doi.org/10.1016/j.anbehav.2014.11.012

Griffin, A. S., Diquelou, M. C., & Perea, M. (2014). Innovative problem solving in birds: A key role of motor diversity. *Animal Behaviour*, *92*, 221–227. https://doi.org/10.1016/j.anbehav.2014.04.009

Griffin, A. S., & Guez, D. (2014). Innovation and problem solving: A review of common mechanisms. *Behavioural Processes*, *109*(PB), 121–134. https://doi.org/10.1016/j.beproc.2014.08.027

Griffin, A. S., & Guez, D. (2016). Bridging the gap between cross-taxon and within-species analyses of behavioral innovations in birds: making sense of discrepant cognition-innovation relationships and the role of motor diversity. In *Advances in the Study of Behavior* (Vol. 48, pp. 1–40). https://doi.org/10.1016/bs.asb.2016.02.001

Griffin, A. S., Guez, D., Lermite, F., & Patience, M. (2013). Tracking changing environments: Innovators are fast, but not flexible learners. *PLoS ONE*, *8*(12). https://doi.org/10.1371/journal.pone.0084907

Griffin, A. S., Guillette, L. M., & Healy, S. D. (2015). Cognition and personality: An analysis of an emerging field. *Trends in Ecology and Evolution*, *30*(4), 207–214. https://doi.org/10.1016/j.tree.2015.01.012

Griffin, A. S., Netto, K., & Peneaux, C. (2017). Neophilia, innovation and learning in an urbanized world: a critical evaluation of mixed findings. *Current Opinion in Behavioral Sciences*. https://doi.org/10.1016/j.cobeha.2017.01.004

Guez, D., & Griffin, A. S. (2016). Unraveling the key to innovative problem solving: a test of learning versus persistence. *Behavioral Ecology*, *27*(5), 1449–1460. https://doi.org/10.1093/beheco/arw055

Guillette, L. M., Hahn, A. H., Hoeschele, M., Przyslupski, A. M., & Sturdy, C. B. (2015). Individual differences in learning speed, performance accuracy and exploratory behaviour in black-capped chickadees. *Animal Cognition*, *18*(1), 165–178. https://doi.org/10.1007/s10071-014-0787-3

Guillette, L. M., Reddon, A. R., Hoeschele, M., & Sturdy, C. B. (2011). Sometimes slower is better: Slow-exploring birds are more sensitive to changes in a vocal discrimination task. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1706), 767–773. https://doi.org/10.1098/rspb.2010.1669

Huebner, F., Fichtel, C., & Kappeler, P. M. (2018). Linking cognition with fitness in a wild primate: Fitness correlates of problem-solving performance and spatial learning ability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756). https://doi.org/10.1098/rstb.2017.0295

Kendal, R. L., Coe, R. L., & Laland, K. N. (2005). Age differences in neophilia, exploration, and innovation in family groups of callitrichid monkeys. *American Journal of Primatology*, *66*(2), 167–188. https://doi.org/10.1002/ajp.20136

Langley, E. J. G., van Horik, J. O., Whiteside, M. A., & Madden, J. R. (2018). Group social rank is associated with performance on a spatial learning task. *Royal Society Open Science*, *5*(2), 171475. https://doi.org/10.1098/rsos.171475

Medina-García, A., Jawor, J. M., & Wright, T. F. (2017). Cognition, personality, and stress in budgerigars, Melopsittacus undulatus. *Behavioral Ecology*, *28*(6), 1504–1516. https://doi.org/10.1093/beheco/arx116

Morand-Ferron, J., Cole, E. F., Rawles, J. E. C., & Quinn, J. L. (2011). Who are the innovators? A field experiment with 2 passerine species. *Behavioral Ecology*, *22*(6), 1241–1248. https://doi.org/10.1093/beheco/arr120

Overington, S. E., Cauchard, L., Côté, K.-A., & Lefebvre, L. (2011). Innovative foraging behaviour in birds: what characterizes an innovator? *Behavioural Processes*, *87*(3), 274–285. https://doi.org/10.1016/j.beproc.2011.06.002

Rowe, C., & Healy, S. D. (2014). Measuring variation in cognition. *Behavioral Ecology*, *25*(6), 1287–1292. https://doi.org/10.1093/beheco/aru090

Shettleworth, S. J. (2010). *Cognition, evolution and behaviour* (2nd ed). New York: Oxford University Press.

Sol, D., Griffin, A. S., & Bartomeus, I. (2012). Consumer and motor innovation in the common myna: The role of motivation and emotional responses. *Animal Behaviour*, *83*(1), 179–188. https://doi.org/10.1016/j.anbehav.2011.10.024

Sorato, E., Zidar, J., Garnham, L., Wilson, A., & Løvlie, H. (2018). Heritabilities and co-variation among cognitive traits in red junglefowl. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756). https://doi.org/10.1098/rstb.2017.0285

Tebbich, S., Stereln, K., & Teschke, I. (2010). The tale of the finch: Adaptive radiation and behavioural flexibility. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1543), 1099–1109. https://doi.org/10.1098/rstb.2009.0291

Thornton, A., & Samson, J. (2012). Innovative problem solving in wild meerkats. *Animal Behaviour*, *83*(6), 1459–1468. https://doi.org/10.1016/j.anbehav.2012.03.018

van Horik, J. O., & Madden, J. R. (2016). A problem with problem solving: Motivational traits, but not cognition, predict success on novel operant foraging tasks. *Animal Behaviour*, *114*, 189–198. https://doi.org/10.1016/j.anbehav.2016.02.006