Otterbein University Digital Commons @ Otterbein

Undergraduate Distinction Papers

Student Research & Creative Work

2016

Cognition and Problem Solving using Detour Reaching and Novel Object Tasks in the Budgerigar

Mollie E. Kemp molliekemp7@gmail.com

Follow this and additional works at: https://digitalcommons.otterbein.edu/stu_dist

Part of the Ornithology Commons, and the Zoology Commons

Recommended Citation

Kemp, Mollie E., "Cognition and Problem Solving using Detour Reaching and Novel Object Tasks in the Budgerigar" (2016). *Undergraduate Distinction Papers*. 29. https://digitalcommons.otterbein.edu/stu_dist/29

This Distinction Paper is brought to you for free and open access by the Student Research & Creative Work at Digital Commons @ Otterbein. It has been accepted for inclusion in Undergraduate Distinction Papers by an authorized administrator of Digital Commons @ Otterbein. For more information, please contact digitalcommons07@otterbein.edu.

Cognition and problem solving using detour reaching and novel object tasks in the budgerigar (Melopsittacus undulatus)

Mollie E. Kemp Department of Biology and Earth Science Otterbein University Westerville, Ohio 43081 5 April 2016

Submitted in partial fulfillment of the requirements for

graduation with Distinction

Advisory Committee:

Anna Young, Ph.D.

Distinction Advisor

David Sheridan, Ph.D.

Second Reader (or Co-advisor if applicable)

Robin Grote, Ph.D.

Distinction Representative

Advisor's Signature

Second Reader's Signature

Distinction Rep's Signature

Abstract

As animal cognition is a complex and multifaceted issue, our understanding of the topic is still incomplete. Particularly, our understanding of what factors may drive the development of intricate and costly behaviors relating to cognition, like bird call or song, are not well understood. One possible explanation is the cognitive capacity hypothesis which states that song complexity is a signal of cognitive abilities and thus an indication of a mate's ability to problem solve and thus effectively provide for offspring and mates. However, previous research of this hypothesis has yielded mixed results and has 1) focused solely on male song or calls and 2) runs on the assumption that problem solving ability is not a function of personality, notably the shyness or boldness of an individual. An individual's place on the shy/bold continuum has been established in previous literature via novel object testing. This study tested problem solving ability and its relation to shyness/boldness in 6 female budgerigars (Melopsittacus undulatus) by utilizing a detour reaching task and novel object task. From these findings, ability to problem solve was not found to be a function of an individual's shyness or boldness. This highlights the need for further investigation into what other factors by be contributing to problem solving ability and how these factors relate to the costly neural investment necessary for bird song and calls.

Introduction

Vocal learning has been postulated to be driven by sexual selection (Nowicki and Searcy, 2004; Searcy and Nowicki, 2000; Mountjoy and Lemon, 1991; Boogert et al. 2011; Verzijden et al. 2012) It is well documented that many avian species prefer mates who have more complex songs or a larger song repertoire (Searcy, 1993; Nowicki and Searcy, 2004; Searcy and Nowicki, 2000; Mountjoy and Lemon, 1991; Boogert et al. 2011). However, what drives this selection and

mate choice remains unknown. The process of learning songs, particularly more complex ones, is very costly in terms of time, energy and neuronal development; in light of these costs, there are still questions of what benefits are associated with learning song (Liker et al. 2005; Peters et al. 2014; Beecher and Brenowitz, 2005; Nowicki et al. 2002). A popular hypothesis is the cognitive capacity hypothesis (Templeton et al. 2014; Boogert et al. 2008) which states that song complexity is a signal of cognitive abilities and thus an indication of a mate's ability to problem solve in order to forage, build a nest, or successfully raise young. Studies attempting to test the cognitive capacity hypothesis have had mixed results.

Previous work on the cognitive capacity hypothesis have focused solely on oscine male song, as a product of sexual selection. This does not offer a functional explanation of female vocal learning at all though. Female bird calls are highly understudied, and thus our understanding of their function is very incomplete (Riebel et al. 2005; Anderson, 2009; Lachlan and Nowicki, 2012). There is still much that can be learned about the function of female song and calls and what it may indicate about the evolution of complex, learned songs or calls in bird species.

In order to test problem solving in birds, it is necessary to assess cognitive ability which requires creative solutions. Finding a successful cognitive testing task must balance the ability of the bird to complete the task without it being too easy or too complex. The tests subjects must also have motivation to complete the task (Laland and Reader, 1999). The examples of such tasks utilized in these experiments are numerous, but often entail some sort of puzzle feeder type device is employed that once solved, yields a food reward to the animal. One very common testing device contains wells containing a food reward covered with a lid (Templeton et al., 2014; Boogert et al., 2008; Leal and Powell 2012a; Cole et al., 2011). These lids may also be

Kemp 3

manipulated in color or pattern, in order to discern discriminatory ability (Leal and Powell, 2012b). Other testing devices may be more complex, such as string pulling devices which open doors or other openings to a reward, or offspring (Isden et al. 2013; Keagy et al. 2009; Krasheninnikova et al. 2013).

Detour reaching tests are another commonly used mode of testing cognition (Amici et al., 2008; Boogert et al., 2011; Santos et al., 1999; Vlamings et al., 2010). In these tasks, an animal is habituated to receiving a food reward from inside an opaque device. Then, an identical but clear device is introduced, and the animal must exhibit inhibitory actions to reach reward. Instead of trying to reach through the clear barrier, the animal must utilize a "detour" to access the reward. This experimental design has been used in diverse taxa, from humans and other primates, to various species of birds such as sparrows (Amici et al., 2008; Boogert et al., 2011; Santos et al., 1999; Vlamings et al., 2010).

Previous assessments of cognition and its functions have focused heavily on its relation to reproductive output. The link between cognition and successful mating has been shown in multiple bird species, such as bowerbirds, *Ptilonorhynchus violaceus*, (Kaegy et al. 2009) and great tits, *Parus major*, (Cauchard et al. 2013). In bowerbirds, males who were more successful at a cognitive test were also more successful at obtaining mates (Kaegy et al. 2009). In a wild population of great tits, problem solving ability was linked with reproductive success. If one or both parents were able to solve a string-pulling type test in order to reach their young, they were also more likely to have higher rates of young reaching fledgling age (Cauchard et al. 2013). However, another study found that male bowerbirds' success at a problem solving tasks, including a novel food source, discriminatory task and spatial memory tasks, was not correlated with the individuals' ability to successfully mate (Isden et al. 2013). European starlings, *Sturnus*

vulgaris, who were more successful at spatial learning also had longer song bout lengths (Farell et al. 2012). There is also evidence that songbirds with more complex, in this case longer, songs have more neural centers in their brains, another indication of greater cognitive capacity (DeVoogd 2004).

Many tests of the cognitive capacity hypothesis have been conducted with the model oscine songbird species, the zebra finch (*Taeniopygia guttata*),in which males sing songs with multiple note elements to court females.Males who had more complex songs were more successful at problem solving a lid flipping task to reach a food reward. The birds who were able to solve this task, or were able to solve it faster, were also those birds who had more complex song qualities (Boogert et al. 2008). Another study utilizing detour reaching, wherein animals have to inhibit reaching for a desired item through a clear barrier and move around it, showed a similar link between tasks solving and song complexity (Boogert et al. 2011). However, one study found no correlation between the problem solving abilities of the individuals and their song complexities. A testing of zebra finches utilizing lid flipping, string pulling and a novel object tasks found no correlation between song complexity and problem solving ability (Templeton et al. 2014).

The investigation into the cognitive capacity hypothesis, as well as the understanding of songs function has yielded muddled results. Many studies and noted how very complex the ties between sexual selection and cognition are (Keagy et al. 2001; Sewall et al. 2015). Sociality, group size, social ranking, personality, and developmental stress may all play into the intricate and multifaceted interactions of sexual selection and cognition (Keagy et al. 2001; Sewall et al. 2001; Sewall et al. 2011; Sewall et al. 2011; Sewall et al. 2011; Sewall et al. 2010; Sewall et al. 2011; Sewall et al. 2011; Sewall et al. 2010; Sewall et al. 2011; Sewall et al. 2011; Sewall et al. 2010; Sewall et al. 2011; Sewall et al. 2010; Sewall et al. 2010; Sewall et al. 2011; Sewall et al. 2010; Sewall et al. 2011; Sewall et al. 2010; Sewall et al. 2010; Sewall et al. 2011; Sewall et al. 2010; Sewall et al. 2011; Sewall et al. 2010; Sewall et al. 2010; Sewall et al. 2011; Sewall et al. 2010; Sewall et al. 2010; Sewall et al. 2011; Sewall et al. 2010; Sewall et al. 2010; Sewall et al. 2011; Sewall et al. 2010; Sewall et al. 2010; Sewall et al. 2011; Sewall et al. 2010; Sewall et al. 2010; Sewall et al. 2011; Sewall et al. 2010; Sewall

Novel object tasks have also been identified as possible test of cognition and problem solving ability, but there is concern that presentation of a novel task does not really test problem solving ability or cognition, but rather personality (Templeton et al. 2014; Carter et al. 2012). Novel objects task are often composed of a new foraging task that the animal has no prior experience with, and must problem solve to reach the food reward. There is a great deal of research to support the idea that when it comes to a novel object, those most likely to approach it are those that are bold within the shy-bold spectrum of personality (Templeton et al. 2014; Sinn et al. 2008; Sloan et al. 1994; Dall 2004; Brown et al. 2005). Therefore, a criticism of presenting novel object tasks is that it may not provide the best opportunity for quantifying an animal's cognitive abilities, and may actually be a test of the animal's personality. However, there have been successful studies utilizing novel object tasks as cognitive tests. Many of these studies have found that those individuals who exhibit greater numbers of exploratory behaviors are more successful problem solvers (Benson-Amram and Holekamp, 2012; Morand-Ferron and Quinn, 2011; Laland and Reader, 1999; Webster and Lefebrve, 2001).

Due to the lack of research and investigation into the function of female song and the mixed results seen to date, the exploration of the cognitive capacity hypothesis and bird cognition in both sexes is still very necessary in order to increase our understanding of the complexities of mate choice and the many signals associated with courtship and eventual reproductive success. Exploration of the cognitive capacity does not only tell us about sexual selection, but has important implications for such as sociality in relation to cognitive ability. Most of the existing work on this topic have made the assumption that personality does not determine or play a significant role in the problem solving abilities of a species (Templeton et al. 2014, Boogert et al. 2011, Boogert et al. 2008). However, there have been few or no attempts to

verify this assumption for the species studied. Before proceeding to evaluating the cognitive capacity hypothesis, it is important that there is supporting evidence for this assumption. The relationship between personality, shyness and boldness and success at cognitive tasks must be well understood to provide accurate testing protocols for investigation into the cognitive capacity hypothesis.

The budgerigar, *Melopsittacus undulatus*, provides an excellent study organism in which to test the cognitive capacity hypothesis. Though they do not have true songs, the budgerigar has a repertoire of contact calls, which are learned and can be large and complex (Dooling et al. 1992; Brown et al. 1988; Lavenex, 1999; Hile et al. 2001). These small, social parrots have been popularly utilized for vocal studies (Dooling et al. 1992; Brown et al. 1988; Brittan-Powell et al. 1997; Farabaugh et al. 1994; Dahlin et al. 2014). The budgerigar is also an ideal choice for this project, as both males and females have contact calls. Using both male and female calls can help to broaden the understanding of the cognitive capacity hypothesis, and has applications past sexual selection, and can give rise to greater understanding of cognition. This study will present budgerigars with problem solving tests and aims to assess cognition. From this, this study hopes to better understand the interface between budgerigar cognition, sociality, and personality and these qualities' complex interface with the function of complex calls, and validate the assumption that neophobia does not co-vary with problem solving. Furthermore, we may better understand what factors may have pressured the evolution of these costly and complex calls.

<u>Methods</u>

Six adult female budgerigars were utilized in this study. Exact age of the birds was unknown, but the birds were acquired approximately two years prior to this study. These females

are housed together in wire mesh cage (70 cm x 60 cm x 50 cm). Sex was determined via genetic testing with PCR. During some phases of these experiment, the birds were separated into single housing cages of wire mesh (70 cm x 60 cm x 50 cm). The cages allowed for vocalizations from other birds to be heard, but did not have visual access to each other (see Figure 1). The birds had access to water and seed diet ad libitum, except when being fasted for experimental phases. During fasting, the birds had free access to water. The budgerigars are housed in 12:12h light and dark cycle, with darkness from 1900hr to 0700hr.

Detour Reaching Testing Devices

Two different sets of devices were used to tests the budgerigars detour reaching ability. Initially, an opaque tubing device was used. This consisted of a solid white PVC pipe of 2.5cm length and 2.3cm in diameter affixed to a wood shim of 19.4cm (Figure 2.) 0.5 grams of a millet reward were then placed inside the device, so that seed was not able to be seen until unless approached by the bird. The second set of devices consisted of 2.5cm of clear plastic tubing with a diameter of 2.5cm. This tubing was slightly flexible but mostly rigid, due to stock and availability. The tubing was attached to a wood shim of 19.4cm (Figure 3.)

Habitation and Experimental Phase

Data was collected from November 1 to December 20 of 2015. Prior to data collection, one opaque device was placed into the group setting for 5 days, in order to allow the birds to acclimate to the object. After this period, habitation to the device and data collection began. Birds were moved into single housing the day before days of data collection. To motivate the birds, food was removed and the birds were fasted from 1800hr to 800hr prior to the start of data collection as well. Ad libitum water was provided at all times. One opaque device was then given

to each bird at 0800hr the following morning, with 0.5 grams of millet inside the tube. Opaque devices were utilized first to shape the behavior of the birds approaching the device and reaching through the open end of the tubes to receive a reward hidden inside. Video recording was utilized for the entirety of the birds' exposure to the device. The birds were given the device for an hour and a half. Then, the device was removed and the birds were given their normal seed diet. The birds either remained in single housing or were returned to the group setting. To minimize stress, data collections were never performed more than two consecutive days, and birds were not individually housed for more than 72 hrs. The habituation phases continued until each bird was consistently accessing the reward via the sides of the opaque tubing, with the exception of one bird who never approached the device or obtained the reward, (Dave, #46). Habituation was completed when the birds were reliably accessing the millet- "solving the task" after five testing days. Following successfully habituation, the detour reaching test was employed utilizing the clear devices. Protocol was same as before, but instead of giving each bird an opaque device, they were given an clear device. Following four separate detour reaching testing days, each birds (with exception of previous bird, #46, who still did not approach device) was reliably solving the task, and data collection ended.

Novel Object Testing

To assess the personality of the birds, novel object testing was utilized. A novel object, a cardboard octagon with a 19.05cm diameter, was affixed to the left side of a cage using zipties (Figure 4). On the ledge of this device (width= 5.08cm) a millet treat reward was placed. To obtain the reward, birds would have to reach into the device. All six females were then selected in random order and placed into the cage individually, with the device for 0.5 hr. Video recording was done throughout.

<u>Analysis</u>

To score each data collection, the videos were watched and scored by one observer. The birds were given a pass or fail grade, depending on whether they obtained the reward. The time to each solving of the puzzle was recorded for each individual bird, and if the bird never solved the device, was given a failing score of 60 minutes. In the clear device stages, number of errors for each bird were also recorded. An error was defined as a bird pecking the tube to try and obtain the reward, instead of going around to the opening to correctly reach the reward.

To analyze the novel object testing, the videos were utilized to record the amount of time that passed before the birds successfully approached the novel object and accessed the reward. If the bird never accessed the reward, they were given a score of 30 minutes, denoting failure. The closest proximity to the device was also recorded. This value, meaning the closest the bird came to the device was recorded via counting the grid number of the cage's mesh on the video, then measuring the experimental cage to obtain the distance from the novel device. If a bird approached the device, the distance was 0cm away, but if the bird never approached the device, then the closest distance away from the device was recorded.

Statistical analysis was preformed, using Excel (Microsoft, 2013.) Pearsons' correlations were run between number of passes with opaque device, number of passes with clear device, time to solve clear device, time to solve opaque device, number of errors with clear device, total exposure to opaque/clear device, time to approach novel object, and object proximity.

<u>Results</u>

For each bird, number of solutions for both clear and opaque devices, as well number of errors in opaque testing are shown in Table 1. Average time to solve the opaque and clear devices are listed in Table 2, no correlation was found between any of these parameters. The summation of information from novel object testing, including time to approach novel object, and proximity to novel object also showed no correlation between any data sets (Table 3). The only significant correlation was found between number of passes during clear device testing and number of passes between opaque device testing (r = 0.84, p = 0.04, Figure 5).

Discussion

This study highlights the complexities in relation to understanding the driving forces behind cognition and vocal learning in birds. Overall, results indicate that the solving of the devices was not random, as the ability to solve the devices was consistent across individual for both opaque and clear devices. However, as this was not correlated with novel object testing, which suggest that cognition in the budgerigar is not driven solely by personality traits. Birds that showed lower abilities to problem solve was not correlated with those who also were most apprehensive to approach a novel object, which suggest that lack of problem solving ability is not a function of neophobia or shyness. This adds to the evidence found in other studies with similar conclusions, that low problem solving ability is not due to shyness or neophobia- but some other factor (Biondi et al. 2010; Griffin and Guez, 2014; Aplin et al. 2008; Boogert et al. 2008b; Griffin and Diquelou, 2015; Griffin et al. 2014; Kendal et al. 2005; Liker and Bokony, 2009; Thorton and Samson, 2012; Webster and Lefevre, 2001.)

An interesting finding was the lack of correlation between the amount of time taken to solve the clear device and the amount of errors made by that bird with the clear device. This could mean that there are alternate strategies for solving the device. Some birds may elect to make few errors, but take longer to solve the device due to lack of exploratory behaviors, while other individuals may make spend more time making errors prior to solving the task but are able to solve it due to their own "trial and error" per se. Other individuals may utilize combinations of these strategies in order to solve the device in the manner that is most adaptive for them.

Another possible factor in relation to problem solving ability is group size. In this study, testing in all phases was done with the budgerigars, a highly social species, were singly housed. Other studies have found that group size was a significant factor in relation to problem solving ability, and those in larger groups were more successful at problem solving tasks (Stowe et al, 2006; Morand-Ferron and Quinn, 2011; Liker and Bokony, 2009). Since this study utilized testing in only groups of one individual, future studies into budgerigar cognition should investigate the impact of larger social settings in regards to problem solving success.

Motivation is also a factor that may be at play in regards to the outcomes of problem solving tasks. Participation by the individuals being tested relies often squarely on their motivation levels, if a bird or other organism is not motivated by hunger or another factor to an adequate level, then it may not participate in that task. This can be problematic as it individuals who may be adept at problem solving may appear to be poor problem solvers simply because they are not motivated enough (Buchanan et al. 2013; Healy et al. 2010).

Cognition is a complex and multifaceted issue, and it is reflected in the existing literature. Many ideas have been purposed, yet no clear hypothesis can be drawn about the drivers of problem solving not only in birds, but across many taxa (see review by Griffin and Geuz, 2014).

Further investigation is needed into this realm of study. This study also focuses on female budgerigars, an often ignored group when studying cognition and its relation with calls and sexual selection. Further enquiry into the problem solving and cognitive abilities and its relation to song in female birds could prove to be a key to understanding what factors may be driving both problem solving ability and song or call investment by birds.

Due to the completion of this work, further investigation of the cognitive capacity, particularly in budgerigars, can be bolstered by the evidence that neophobia is not a factor contributing to cognitive ability. Call complexity and problem solving ability can then be utilized to assess the cognitive capacity hypothesis in both male and female budgerigars- and could provide great insight into the drivers for complex call investment.

Acknowledgements

This project would not have been possible without the support of Otterbein's Biology and Earth Science department. The cost of this project was supported through Otterbein's Student Research Fund. Perhaps the most gratitude to Dr. Anna Young for her never ending wisdom and advice- as well as encouragement when I needed it the most. Special thanks go out to the Young lab for editing, revisions and general insight, including Rachel Dalton, Samantha Perry, Matthew Veith, Abigail Smith, Delaney Gailbraith, Meaghan Graver, Kelly Jackson, and Liza Hanes. I would also like to thank Dr. Aaron Reinhard for his help in the mechanics of creating the devices. Additionally, thanks to Dr. David Sheridan and Dr. Robin Grote for their participation as members of my distinction committee. Finally, a word of thanks for my feathered participants, who made this study possible via their participation (or lack thereof) and in the process doled out many a lesson about the challenges and joys of working with live animals.



Figure 1. Cage set up is shown above. For testing phases described in methods, each bird was placed separately into a single housing cage. Birds could hear each other, but as can be seen from the photo, had no visual access to other birds.



Figure 2. Opaque Testing Device. Millet reward was placed in the tube, so that it was only accessible by going around and reaching through either open end.



Figure 3. Clear testing device is shown. Millet was placed within the tube, so that it was only accessible by reaching in through the open ends. Errors were recorded when birds tried to peck through the top the of the tube to reach the reward within.



Figure 4. Novel object testing device, affixed to left side of cage and perpendicular to perch. Millet reward was placed on inner ledge as shown. Device was "solved" when bird successfully reached in to obtain device.

Bird Name and Band Number	No. of Solutions- Opaque	No. of Solutions- Clear	No. of errors- clear
Ludwig #42	3	3	0
Ernie #44	2	4	2
Dave #46	0	0	0
Emu #47	3	3	2
Darwin #48	4	4	1
Robin #49	1	2	2

Table 1. Each bird's specific name and band number is listed, along with the total number of solutions for both the opaque and clear testing devices. Total number of errors made during all clear testing is also listed. Clear errors are only listed due to the impossibility of trying to reach through opaque device to reach reward- i.e. the birds can only make errors in clear device stage.

Bird Name and Band Number	Average Time to Solve (minutes) Opaque	Average Time to Solve (minutes) Clear
Ludwig #42	34.46	25.28
Ernie #44	54.89	15.75
Dave #46	60	60
Emu #47	39.39	28.71
Darwin #48	26.36	16.69
Robin #49	58.06	36.64

Table 2. Bird name and band number are shown with the average amount of time it took that individual to solve both the opaque and clear devices. Time is given in minutes. A time of 60 minutes denotes failure- the bird never solved the task, nor reached the food reward.

Bird Name and Band Number	Time to Approach Novel Object (minutes)	Proximity to Novel Object (cm)
Ludwig #42	25.52	0.0
Ernie #44	30.0	31.0
Dave #46	30.0	37.0
Emu #47	30.0	33.5
Darwin #48	7.58	0.0
Robin #49	14.37	0.0

Table 2. Bird name and band number are shown with the amount of time in minutes that elapsed before the bird approached the novel object and obtained reward. A time of 30.0 denotes failure, bird did not approach the device nor receive reward. Proximity to novel object is also shown, in centimeters. If bird did approach the novel object, proximity was 0.0.



Figure 5. Number of passes for clear device testing and number of passes for opaque device testing are correlated (p-value=0.84232.) Each data point represents and individual bird.

<u>References</u>

- Airey DC and DeVoogd TJ. 2000. Greater song complexity is associated with augmented song system anatomy in zebra finches. Neuroreport 11(8):1749-54.
- Amici F, Aureli F, Call J. 2008. Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. Current Biology 18(18):1415-9.
- Anderson RC. 2009. Operant conditioning and copulation solicitation display assays reveal a stable preference for local song by female swamp sparrows melospiza georgiana. Behav Ecol Sociobiol 64(2):215-23.
- Aplin LM, Sheldon BC, Morand-Ferron J. 2013. Milk bottles revisited: Social learning and individual variation in the blue tit, cyanistes caeruleus. Anim Behav 85(6):1225-32.
- Beecher MD and Brenowitz EA. 2005. Functional aspects of song learning in songbirds. Trends in Ecology & Evolution 20(3):143-9.
- Benson-Amram S and Holekamp KE. 2012. Innovative problem solving by wild spotted hyenas. Proc Biol Sci 279(1744):4087-95.
- Biondi LM, Bó MS, Vassallo AI. 2010. Inter-individual and age differences in exploration, neophobia and problem-solving ability in a neotropical raptor (milvago chimango). Animal Cognition 13(5):701-10.
- Bókony V, Lendvai ÁZ, Vágási CI, Patras L, Pap PL, Németh J, Vincze E, Papp S, Preiszner B, Seress G, et al. 2014. Necessity or capacity? physiological state predicts problem-solving performance in house sparrows. Behavioral Ecology 25(1):124-35.
- Boogert NJ, Fawcett TW, Lefebvre L. 2011. Mate choice for cognitive traits: A review of the evidence in nonhuman vertebrates. Behav Ecol 22(3):447-59.
- Boogert NJ, Reader SM, Hoppitt W, Laland KN. 2008. The origin and spread of innovations in starlings. Anim Behav 75(4):1509-18.
- Boogert NJ, Anderson RC, Peters S, Searcy WA, Nowicki S. 2011. Song repertoire size in male song sparrows correlates with detour reaching, but not with other cognitive measures. Anim Behav 81(6):1209-16.
- Boogert NJ, Giraldeau L, Lefebvre L. 2008. Song complexity correlates with learning ability in zebra finch males. Anim Behav 76(5):1735-41.
- Boogert NJ, Reader SM, Laland KN. 2006. The relation between social rank, neophobia and individual learning in starlings. Anim Behav 72(6):1229-39.

- Brittan-Powell E, Dooling RJ, Farabaugh SM. 1997. Vocal development in budgerigars (*melopsittacus undulatus*): Contact calls. Journal of Comparative Psychology 111(3):226-41.
- Brittan-Powell EF, Dooling RJ, Farabaugh SM. 1997. Vocal development in budgerigars (melopsittacus undulatus): Contact calls. Journal of Comparative Psychology 111(3):226.
- Brown SD, Dooling RJ, O'Grady KE. 1988. Perceptual organization of acoustic stimuli by budgerigars (melopsittacus undulatus): III. contact calls. Journal of Comparative Psychology 102(3):236.
- Brown C, Jones F, Braithwaite V. 2005. In situ examination of boldness–shyness traits in the tropical poeciliid, brachyraphis episcopi. Anim Behav 70(5):1003-9.
- Buchanan KL, Grindstaff JL, Pravosudov VV. 2013. Condition dependence, developmental plasticity, and cognition: Implications for ecology and evolution. Trends in Ecology & Evolution 28(5):290-6.
- Carazo P, Noble DWA, Chandrasoma D, Whiting MJ. 2014. Sex and boldness explain individual differences in spatial learning in a lizard. Proc Biol Sci 281(1782):20133275-.
- Carter AJ, Marshall HH, Heinsohn R, Cowlishaw G. 2014. Personality predicts the propensity for social learning in a wild primate. Peerj 2:e283-.
- Carter AJ, Marshall HH, Heinsohn R, Cowlishaw G. 2012. How not to measure boldness: Novel object and antipredator responses are not the same in wild baboons. Anim Behav 84(3):603-9.
- Cauchard L, Boogert NJ, Lefebvre L, Dubois F, Doligez B. 2013. Problem-solving performance is correlated with reproductive success in a wild bird population. Anim Behav 85(1):19-26.
- Cole EF and Quinn JL. 2012. Personality and problem-solving performance explain competitive ability in the wild. Proceedings of the Royal Society B: Biological Sciences 279(1731):1168-75.
- Cole EF, Cram DL, Quinn JL. 2011. Individual variation in spontaneous problem-solving performance among wild great tits. Anim Behav 81(2):491-8.
- Cronin KA, Kurian AV, Snowdon CT. 2005. Cooperative problem solving in a cooperatively breeding primate (saguinus oedipus). Anim Behav 69(1):133-42.
- Dahlin CR, Young AM, Cordier B, Mundry R, Wright TF. 2014. A test of multiple hypotheses for the function of call sharing in female budgerigars, melopsittacus undulatus. Behav Ecol Sociobiol 68(1):145-61.

- Dall SRX. 2004. Behavioural biology: Fortune favours bold and shy personalities. Current Biology 14(12):R470-2.
- DeVoogd TJ. 2004. Neural constraints on the complexity of avian song. Brain, Behavior and Evolution 63(- 4):- 221.
- Dooling RJ, Brown SD, Klump GM, Okanoya K. 1992. Auditory perception of conspecific and heterospecific vocalizations in birds: Evidence for special processes. Journal of Comparative Psychology 106(1):20.
- Dooling RJ, Park TJ, Brown SD, Okanoya K, Soli SD. 1987. Perceptual organization of acoustic stimuli by budgerigars (*melopsittacus undulatus*): II. vocal signals. Journal of Comparative Psychology 101(4):367-81.
- Emery NJ and Clayton NS. 2009. Tool use and physical cognition in birds and mammals. Curr Opin Neurobiol 19(1):27-33.
- Farabaugh SM, Brown ED, Dooling RJ. 1992. Analysis of warble song of the budgerigar melopsittacus undulatus. Bioacoustics 4(2):111-30.
- Farabaugh SM, Linzenbold A, Dooling RJ. 1994. Vocal plasticity in budgerigars (*melopsittacus undulatus*): Evidence for social factors in the learning of contact calls. Journal of Comparative Psychology 108(1):81-92.
- Farrell TM, Weaver K, An Y, MacDougall-Shackleton SA. 2012. Song bout length is indicative of spatial learning in european starlings. Behavioral Ecology 23(1):101-11.
- Griffin AS and Diquelou MC. 2015. Innovative problem solving in birds: A cross-species comparison of two highly successful passerines. Anim Behav 100:84-94.
- Griffin AS and Guez D. 2014. Innovation and problem solving: A review of common mechanisms. Behav Processes 109(Pt B):121-34.
- Griffin AS, Diquelou M, Perea M. 2014. Innovative problem solving in birds: A key role of motor diversity. Anim Behav 92:221-7.
- Healy SD, Haggis O, Clayton NS. 2010. Zebra finches and cognition. Emu 110(3):242-50.
- Hile AG, Plummer TK, Striedter GF. 2000. Male vocal imitation produces call convergence during pair bonding in budgerigars, melopsittacus undulatus. Anim Behav 59(6):1209-18.
- Hile AG, Plummer TK, Striedter GF. 2000. Male vocal imitation produces call convergence during pair bonding in budgerigars, melopsittacus undulatus. Anim Behav 59(6):1209-18.
- Holekamp KE. 2007. Questioning the social intelligence hypothesis. Trends Cogn Sci (Regul Ed) 11(2):65-9.

- Isden J, Panayi C, Dingle C, Madden J. 2013. Performance in cognitive and problem-solving tasks in male spotted bowerbirds does not correlate with mating success. Anim Behav 86(4):829-38.
- Keagy J, Savard J, Borgia G. 2011. Complex relationship between multiple measures of cognitive ability and male mating success in satin bowerbirds, ptilonorhynchus violaceus. Anim Behav 81(5):1063-70.
- Keagy J, Savard J, Borgia G. 2009. Male satin bowerbird problem-solving ability predicts mating success. Anim Behav 78(4):809-17.
- Kendal R, Coe R, Laland K. 2005. Age differences in neophilia, exploration, and innovation in family groups of callitrichid monkeys. Am J Primatol 66(2):167.
- Lachlan R and Nowicki S. 2012. How reliable is song learning accuracy as a signal of male early condition? Am Nat 180(6):751-61.
- Laland K and Reader S. 1999. Foraging innovation in the guppy. Anim Behav 57:331-40.
- Lampe HM and Saetre G. 1995. Female pied flycatchers prefer males with larger song repertoires. Proceedings of the Royal Society of London Series B: Biological Sciences 262(1364):163-7.
- Lavenex PB. 1999. Vocal production mechanisms in the budgerigar (melopsittacus undulatus): The presence and implications of amplitude modulation. J Acoust Soc Am 106(1):491-505.
- Leal M and Powell BJ. 2012. Behavioural flexibility and problem-solving in a tropical lizard. Biology Letters 8(1):28-30.
- Leal M and Powell BJ. 2012. On the flexibility of lizards' cognition: A response to vasconcelos et al. Biology Letters 8(1):44-5.
- Liker A and Székely T. 2005. Mortality costs of sexual selection and parental care in natural populations of birds. Evolution 59(4):890-7.
- Liker A and Bókony V. 2009. Larger groups are more successful in innovative problem solving in house sparrows. Proceedings of the National Academy of Sciences 106(19):7893-8.
- Morand-Ferron J and Quinn JL. 2011. Larger groups of passerines are more efficient problem solvers in the wild. Proc Natl Acad Sci U S A 108(38):15898-903.
- Mountjoy DJ and Lemon RE. 1991. Song as an attractant for male and female european starlings, and the influence of song complexity on their response. Behav Ecol Sociobiol 28(2):97-100.

- Nowicki S, Searcy W, Peters S. 2002. Brain development, song learning and mate choice in birds: A review and experimental test of the" nutritional stress hypothesis". Journal of Comparative Physiology A 188(11-12):1003-14.
- Nowicki S and Searcy WA. 2004. Song function and the evolution of female preferences: Why birds sing, why brains matter. Ann N Y Acad Sci 1016(1):704-23.
- Peters S, Searcy WA, Nowicki S. 2014. Developmental stress, song-learning, and cognition. Integrative and Comparative Biology 54(4):555-67.
- Riebel K, Hall M, Langmore N. 2005. Female songbirds still struggling to be heard. Trends Ecol Evol 20(8):419-20.
- Santos LR, Ericson BN, Hauser MD. 1999. Constraints on problem solving and inhibition: Object retrieval in cotton-top tamarins (saguinus oedipus oedipus). Journal of Comparative Psychology 113(2):186.
- Searcy W and Nowicki S. 2000. Male-male competition and female choice in the evolution of vocal signaling. Animal Signals: Signalling and Signal Design in Animal Communication :301-15.
- Searcy WA. 1992. Song repertoire and mate choice in birds. American Zoologist 32(1):71-80.
- Seed AM and Call J. 2010. Problem-solving in tool-using and non-tool-using animals. In: Encyclopedia of animal behavior. Moore MDB, editor. Oxford: Academic Press. 778 p.
- Sewall KB, Soha JA, Peters S, Nowicki S. 2013. Potential trade-off between vocal ornamentation and spatial ability in a songbird. Biol Lett 9(4):20130344.

Shettleworth SJ. 2001. Animal cognition and animal behaviour. Anim Behav 61(2):277-86.

- Sinn DL, Gosling SD, Moltschaniwskyj NA. 2008. Development of shy/bold behaviour in squid: Context-specific phenotypes associated with developmental plasticity. Anim Behav 75(2):433-42.
- Sloan Wilson D, Clark AB, Coleman K, Dearstyne T. 1994. Shyness and boldness in humans and other animals. Trends in Ecology & Evolution 9(11):442-6.
- Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L. 2005. Big brains, enhanced cognition, and response of birds to novel environments. Proceedings of the National Academy of Sciences of the United States of America 102(15):5460-5.
- Soma M and Garamszegi LZ. 2011. Rethinking birdsong evolution: Meta-analysis of the relationship between song complexity and reproductive success. Behavioral Ecology.

- Stöwe M, Bugnyar T, Heinrich B, Kotrschal K. 2006. Effects of group size on approach to novel objects in ravens (corvus corax). Ethology 112(11):1079-88.
- Stöwe M, Bugnyar T, Heinrich B, Kotrschal K. 2006. Effects of group size on approach to novel objects in ravens (corvus corax). Ethology 112(11):1079-88.
- Stöwe M, Bugnyar T, Loretto M, Schloegl C, Range F, Kotrschal K. 2006. Novel object exploration in ravens (corvus corax): Effects of social relationships. Behav Processes 73(1):68-75.
- Templeton CN, Laland KN, Boogert NJ. 2014. Does song complexity correlate with problemsolving performance in flocks of zebra finches? Anim Behav 92:63-71.
- Thornton A and Samson J. 2012. Innovative problem solving in wild meerkats. Anim Behav 83(6):1459-68.
- Thornton A and Lukas D. 2012. Individual variation in cognitive performance: Developmental and evolutionary perspectives. Philosophical Transactions of the Royal Society b-Biological Sciences 367(1603):2773-83.
- Thornton A and Samson J. 2012. Innovative problem solving in wild meerkats. Anim Behav 83(6):1459-68.
- Tu H, Smith EW, Dooling RJ. 2011. Acoustic and perceptual categories of vocal elements in the warble song of budgerigars (melopsittacus undulatus). Journal of Comparative Psychology 125(4):420.
- Verzijden MN, ten Cate C, Servedio MR, Kozak GM, Boughman JW, Svensson EI. 2012. The impact of learning on sexual selection and speciation. Trends in Ecology & Evolution 27(9):511-9.
- Vlamings PH, Hare B, Call J. 2010. Reaching around barriers: The performance of the great apes and 3–5-year-old children. Animal Cognition 13(2):273-85.
- von Bayern AMP, Heathcote RJP, Rutz C, Kacelnik A. 2009. The role of experience in problem solving and innovative tool use in crows. Current Biology 19(22):1965-8.
- Webster SJ and Lefebvre L. 2001. Problem solving and neophobia in a columbiform– passeriform assemblage in barbados. Anim Behav 62(1):23-32.
- Webster S and Lefebvre L. 2001. Problem solving and neophobia in a columbiform-passeriform assemblage in barbados. Anim Behav 62:23-32.
- Werdenich D and Huber L. 2006. A case of quick problem solving in birds: String pulling in keas, nestor notabilis. Anim Behav 71(4):855-63.