Peer Community In Ecology

How would variation in environmental predictability affect the use of different learning mechanisms in a social bird?

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Aliza le Roux based on reviews by Matthew Petelle and 1 anonymous reviewer

A recommendation of:

Kelsey McCune, Richard McElreath, Corina Logan. **Investigating the use of learning mechanisms in a species that is rapidly expanding its geographic range** *(2019). In Principle Recommendation by Peer Community In Ecology.* http://corinalogan.com/Preregistrations/g_sociallearning.html

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Aliza le Roux (2019) How would variation in environmental predictability affect the use of different learning mechanisms in a social bird?. *Peer Community in Ecology, 100032.* 10.24072/pci.ecology.100032

In their pre-registered paper [1], McCune and colleagues propose a field-based study of social versus individual learning mechanisms in an avian species (great-tailed grackles) that has been expanding its geographic range. The study forms part of a longer-term project that addresses various aspects of this species' behaviour and biology, and the experience of the team is clear from the preprint.

Assessing variation in learning mechanisms in different sections of the grackles' distribution range, the researchers will investigate how individual learning and social transmission may impact learning about novel challenges in the environment. Considering that this is a social species, the authors expect both individual learning and social transmission to occur, when groups of grackles encounter new challenges/ opportunities in the wild. This in itself is not a very unusual idea to test [2, 3], but the authors are rigorously distinguishing between imitation, emulation, local enhancement, and social enhancement. Such rigour is certainly valuable in studies of cognition in the wild. Further, the authors predict that the contribution of individual versus social learning could vary between populations, as the core may contain fewer unfamiliar/novel stimuli than the edge, where artificial sources of water (for example) may be more common. They make an argument that the core, middle, and edge populations would experience differing levels of environmental predictability. If true, their field experiments could yield very novel results on how changes in environmental predictability affect social/individual learning in a single study species. Their data would then give unusual insights into the ecological value of individual learning and distinct forms of social learning – something that is not easy to test in wild animals. The authors consider a variety of alternative hypotheses that may ultimately explain their findings, and clarify their methods and analyses in fine detail. The authors also set out limitations clearly, and give a thorough account of their approaches and thinking. The reviewers and I have a still-unanswered question, which is central to the study: what is the predictability or unpredictability of the core versus edge environments? Although the authors have explained similarities and distinctions between the different sections of the grackles' range, their description feels a bit vague -- it's not as rigorous or well-defined as the rest of the paper. Such a lack of definition may be inevitable in the limitations of a preprint, but ultimately it does suggest that there may be real uncertainty about the qualitative differences between the core, edge, and middle environments. The authors do explain that a lack of variation in individual responses to the field experiments would preclude the testing of further hypothesis, but do not mention how a salient lack of variation in novelty/ predictability between the environments could impact their hypotheses. An assessment/quantification of

the rate at which the different populations of grackles encounter novel stimuli would be a cornerstone of the success of this proposed study. Certainly, the authors cannot address this in much more detail during the preprint stage, but they need to consider how to best assess/describe differences before starting the full study. Such an assessment could take the form of either a GIS desktop study (comparing, for example, rates of dam/canal construction in core versus edge sections of the distribution range), or observational/ movement data contrasting how frequently members of core versus edge populations encounter artificial sources of water/food in a given month/year. Considering the long-term nature of the larger project, it is possible that these data are already available, but I am speculating. I would highly recommend that such an assessment be undertaken, beyond the mere mention of expected differences. This would solidify the central idea that there are concrete differences between the environments. Despite this concern, the authors attended well to the comments and recommendations of the two reviewers – both experts in cognitive ecology. It is a preprint showing clear thinking and a consideration of most of the challenges that may be encountered during the course of the study. My own opinion and the estimations of the two reviewers all underscore the originality and value of this project – this should be a very valuable and potentially novel study. I look forward to seeing the outcomes of the research.

References

[1] McCune, K. B., McElreath, R., and Logan, C. J. (2019). Investigating the use of learning mechanisms in a species that is rapidly expanding its geographic range. In principle recommendation by Peer Community In Ecology. corinalogan.com/Preregistrations/g_sociallearning.html [2] Benson-Amram, S. and Holekamp, K. E. (2012). Innovative problem solving by wild spotted hyenas. Proceedings of the Royal Society B: Biological Sciences, 279(1744), 4087–4095. doi: 10.1098/rspb.2012.1450 [3] Federspiel, I. G., Boeckle, M., von Bayern, A. M. P. and Emery, N. J. (2019). Exploring individual and social learning in jackdaws (Corvus monedula). Learning & Behavior, 47(3), 258–270. doi: 10.3758/s13420-019-00383-8

Revision round #1

2019-09-13

I have now obtained two reviews of the pre-registered study focusing on cognition in birds encountering novel environments. Both reviewers (and I) found the study to be interesting, relevant, and well-planned. It is very close to being recommended, but I think the changes suggested by the two reviewers merit inclusion. They will improve the study and allow the authors to pay attention to additional factors that they have not yet considered. Therefore, I would like the authors to attend to the revisions suggested below, and resubmit the pre-registration. I do not think that it will require another full round of reviews, and as recommender, I will assess whether or not the authors have addressed these points sufficiently.

Reviewer #1 This pre-registered study is very interesting and could be very informative to several fields including cognition and invasion biology. The hypotheses are clearly stated, and multiple predictions are presented. The authors have certainly thought about this extensively. I do have a few small issues that I think the authors should try to consider going forward.

The three populations represent the core, middle, and edge of the range expansion. The idea is that these populations could differ in their flexibility, however, another option that could explain differences between populations are levels of urbanization. I'm not sure about the core population, but it seems that the middle and edge populations are found in urban areas. Have the authors thought about testing rural areas outside of their urban zones? This could help control for potential habitat sorting by personality and/or flexibility.

Many bird species (especially corvids and parrots) are notoriously neophobic. Have the authors thought about having a cutoff point (trials/time) where birds are no longer part of the experiment because logistics?

I have one further comment about repeatability. Although two measures of flexibility is better than one to estimate repeatability. Three measures would be

better to get a better estimate of the residual error (the within individual variance).

Otherwise, I am looking forward to the papers that result from this study.

Reviewer #2 Here, I review the pre-registered study “Investigating the use of learning mechanisms in a species that is rapidly expanding its geographic range” by Dr McCune et al. The study will adopt an intraspecific approach, focussing on the great-tailed grackle, and in doing so use a novel methodology to determine the cognitive mechanisms underpinning the geographic expansion of species. The hypotheses are very clearly laid out, and the authors provide a detailed description of the analyses they will perform (including the R code). However, I do believe more information is needed at certain points; particularly when justifying the rationale for the study, and in the methods section. Overall, I find the study very interesting, well thought-out, and timely.

Major points The study seems to assume that in expanding their geographic range, the study species will encounter new environments, and thus novel challenges. First, I think much more detail is needed on the new environments that will be encountered (and any specific differences between edge, middle, and core populations). Following this, it needs to be more clearly elucidated how these new environments will provide novel challenges. Given that this is central to the investigation, this information is crucial in justifying the experiment and its predictions. In parts I find the methods section is lacking in detail. I find the definition of group quite vague; “a group is defined as having the same trained demonstrator(s) in the presence of many of the same conspecifics” – what constitutes ‘many’ and are you confident that enough of the same individuals will be present across multiple sessions? I also believe this is why a ‘study species’ section in the methods would be beneficial; what is the grackles social system? Do they live in stable groups? As someone who is not familiar with this study system, the suitability of it is unclear. I also think more information in the text is needed on each of the solving techniques, rather than trying to infer from Fig. 1.

Minor points An alternative to P2 could be a ‘necessity drives innovation’ mechanism, whereby subordinates outperform dominants (similar to what has

been found in meerkats on problem-solving tasks). How many demonstrators will there be per group? How confident can you be that observers from each group will not be exposed to other demonstrators using different opening methods? (particularly if you are unsure which birds will be at which group). Do you have an indication for the number of birds per group? I realise this is difficult considering group size may fluctuate, and you may not have completed banding. But it will be informative in terms of assessing the power of analyses for the core and edge sites where you only have one group at each. Presumably you will record the trials? What software will you use to score the trials?

Thank you for the interesting submission!

Preprint DOI: http://corinalogan.com/Preregistrations/g_sociallearning.html

Reviewed by Matthew Petelle, 2019-08-06 15:54

PCI Ecol review of pre-registered study: Investigating the use of learning mechanisms in a species that is rapidly expanding its geographic range

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Many bird species (especially corvids and parrots) are notoriously neophobic. Have the authors thought about having a cutoff point (trials/time) where birds are no longer part of the experiment because logistics?

I have one further comment about repeatability. Although two measures of flexibility is better than one to estimate repeatability. Three measures would be better to get a better estimate of the residual error (the within individual variance).

Otherwise, I am looking forward to the papers that result from this study.

Reviewed by anonymous reviewer, 2019-09-11 10:08

Here, I review the pre-registered study "Investigating the use of learning mechanisms in a species that is rapidly expanding its geographic range" by Dr McCune et al. The study will adopt an intraspecific approach, focussing on the great-tailed grackle, and in doing so use a novel methodology to determine the cognitive mechanisms underpinning the geographic expansion of species. The hypotheses are very clearly laid out, and the authors provide a detailed description of the analyses they will perform (including the R code). However, I do believe more information is needed at certain points; particularly when justifying the rationale for the study, and in the methods section. Overall, I find the study very interesting, well thought-out, and timely.

Major points The study seems to assume that in expanding their geographic range, the study species will encounter new environments, and thus novel challenges. First, I think much more detail is needed on the new environments that will be encountered (and any specific differences between edge, middle, and core populations). Following this, it needs to be more clearly elucidated how these new environments will provide novel challenges. Given that this is central to the investigation, this information is crucial in justifying the experiment and its predictions. In parts I find the methods section is lacking in detail. I find the definition of group quite vague; "a group is defined as having the same trained demonstrator(s) in the presence of many of the same conspecifics" – what constitutes 'many' and are you confident that enough of the same individuals will be present across multiple sessions? I also believe this is why a 'study species' section in the methods would be beneficial; what is the grackles social system? Do they live in stable groups? As someone who is not familiar with this study system,

the suitability of it is unclear. I also think more information in the text is needed on each of the solving techniques, rather than trying to infer from Fig. 1.

Minor points An alternative to P2 could be a 'necessity drives innovation' mechanism, whereby subordinates outperform dominants (similar to what has been found in meerkats on problem-solving tasks). How many demonstrators will there be per group? How confident can you be that observers from each group will not be exposed to other demonstrators using different opening methods? (particularly if you are unsure which birds will be at which group). Do you have an indication for the number of birds per group? I realise this is difficult considering group size may fluctuate, and you may not have completed banding. But it will be informative in terms of assessing the power of analyses for the core and edge sites where you only have one group at each. Presumably you will record the trials? What software will you use to score the trials?

Author's reply:

Dear Dr.'s le Roux and Petelle, and an anonymous reviewer,

We greatly appreciate the time you have taken to give us such useful feedback! We are very thankful for your willingness to participate in the peer review of preregistrations, and we are happy to have the opportunity to revise and resubmit. We revised our preregistration and associated files at http://corinalogan.com/Preregistrations/g*sociallearning.html, and we responded to your comments (which we numbered for clarity) below. Note that the version-tracked version of this preregistration is in rmarkdown at GitHub: https://github.com/corinalogan/grackles/blob/master/Files/Preregistrations/g*sociallearning.Rmd. In case you want to see the history of track changes for this document at GitHub, click the previous link and then click the "History" button on the right near the top. From there, you can scroll through our comments on what was changed for each save event and if you want to see exactly what was changed, click on the text that describes the change and it will show you the text that was replaced (in red) next to the new text (in green). We think the revised version is much improved due to your generous feedback!

All our best, Kelsey, Richard, and Corina

Investigating the use of learning mechanisms in a species that is rapidly expanding its geographic range

Dr. Kelsey McCune, Dr. Richard McElreath, Dr. Corina Logan

Reviewer #1 Matthew Petelle

Comment 1: This pre-registered study is very interesting and could be very informative to several fields including cognition and invasion biology. The hypotheses are clearly stated, and multiple predictions are presented. The authors have certainly thought about this extensively. I do have a few small issues that I think the authors should try to consider going forward. The three populations represent the core, middle, and edge of the range expansion. The idea is that these populations could differ in their flexibility, however, another option that could explain differences between populations are levels of urbanization. I'm not sure about the core population, but it seems that the middle and edge populations are found in urban areas. Have the authors thought about testing rural areas outside of their urban zones? This could help control for potential habitat sorting by personality and/or flexibility.

Response 1: Thank you for your positive feedback! In answer to your question about urbanization, eBird data indicates that all great-tailed grackle sightings occur in relatively human-dominated areas. The Birds of North America species account states that grackles across the range are very attracted to urban and agricultural sources of food (Johnson and Peer 2001). We are conducting focal follows on all banded grackles to measure foraging behavior and habitat preferences (described in this separate preregistration: http://corinalogan.com/Preregistrations/g_flexforaging.html), so we can test whether the foraging environment is similar in our populations. During focal follows we measure the preference of each grackle for different substrates (cement, grass, trees, dumpsters, etc), the distance of grackles to human-provided food sources (dumpsters, outdoor cafes, agricultural areas), and the number of human-provided food sources within each grackle's home range. As a result, we should be able to determine whether differences in performance in the social

learning task stem from population-level differences in urbanization that affect flexibility, personality, individual learning or social learning.

Comment 2: Many bird species (especially corvids and parrots) are notoriously neophobic. Have the authors thought about having a cutoff point (trials/time) where birds are no longer part of the experiment because logistics?

*Response 2: This is a good point! We are time-limited because we are conducting research in 3 populations sequentially over 5 years, thus to ameliorate neophobia we will implement apparatus habituation. Before we begin trials, we will give each group time to habituate to each apparatus in a non-functional form. This should help decrease the effects of neophobia during the actual trials. We will only conduct eight 45 min long social learning trials in each group, so there likely will be some individuals that do not participate and this may decrease our power to detect social learning mechanisms. However, given our experience habituating grackles in Arizona to our traps, we know that at least some grackles (in addition to our trained demonstrators) will be comfortable manipulating the apparatus.

We have clarified our habituation and experimental design in METHODS > Data collection stopping rule. Our revised text is below for your convenience: “Each group will be given time to habituate to non-functional apparatuses prior to starting social learning trials. We will put out the apparatuses with food on and around them until the majority of grackles are eating comfortably. Each locus on the apparatuses will be disabled during this habituation period so that grackles cannot learn solving methods. During social learning trials, we will conduct a maximum of eight sessions of up to 45 minutes per apparatus type per group.”*

Comment 3: I have one further comment about repeatability. Although two measures of flexibility is better than one to estimate repeatability. Three measures would be better to get a better estimate of the residual error (the within individual variance).

*Response 3: This is a great point. We agree that three measures for repeatability is better than two. We had originally planned to have three measures for flexibility: reversal learning on the color tubes, reversal learning on the

touchscreen, and solution switching on the multi-access box (see separate preregistration for more details: http://corinalogan.com/Preregistrations/g_flexmanip.html). However, reversal learning on the touchscreen experiment did not appear to measure what it was intended to measure. It is confounded and we don't have time to conduct the in-depth experiments to determine what is going wrong. Thus, we now dropped the touchscreen reversal learning experiment and replaced it with a second multi-access box: the log apparatus in the learning mechanism experiment, so we will continue to have three measures of flexibility (see State of the Data in the preregistration linked above for more details).

However, we suspect your comment about repeatability here refers not to flexibility, but to the repeatability of which learning mechanisms individuals rely on in Hypothesis 3 in the preregistration you reviewed. We assess the use of learning mechanisms on two different apparatus types that have both been previously used on other species, thus allowing us to make direct cross-species comparisons of performance. Unfortunately, we will not have enough time to design and run a third apparatus type due to the extensive amount of time we invest in color marking grackles at each site (it's taken 2 years to band 60 grackles in Arizona) before we are able to begin the learning mechanism experiment. Additionally, we will need to conduct the experiment before the breeding season begins in March so that the grackles will actually pay attention to the apparatus. At the next two field sites (where we will be for one year each), this will leave us ~3 months to color mark all grackles (we primarily trap in the non-breeding season so as not to interfere with parental care), and ~2 months to conduct the experiment. We think this is already pushing our time limits so we have opted to test only two apparatus types.*

Comment 4: Otherwise, I am looking forward to the papers that result from this study.

Response 4: Thank you so much for your constructive criticism. We appreciate your help in making this a better study.

Reviewer #2:

Comment 5: Here, I review the pre-registered study "Investigating the use of learning mechanisms in a species that is rapidly expanding its geographic range" by Dr McCune et al. The study will adopt an intraspecific approach, focussing on the great-tailed grackle, and in doing so use a novel methodology to determine the cognitive mechanisms underpinning the geographic expansion of species. The hypotheses are very clearly laid out, and the authors provide a detailed description of the analyses they will perform (including the R code). However, I do believe more information is needed at certain points; particularly when justifying the rationale for the study, and in the methods section. Overall, I find the study very interesting, well thought-out, and timely.

Response 5: Thank you for these kind words, and we are happy to address your concerns to improve the quality of this study.

Comment 6: The study seems to assume that in expanding their geographic range, the study species will encounter new environments, and thus novel challenges. First, I think much more detail is needed on the new environments that will be encountered (and any specific differences between edge, middle, and core populations). Following this, it needs to be more clearly elucidated how these new environments will provide novel challenges. Given that this is central to the investigation, this information is crucial in justifying the experiment and its predictions.

*Response 6: This is a good point. We failed to make explicit that there are major differences in climate across the three populations that lead to novel challenges for maintaining homeostasis, finding nesting substrates, and foraging on natural food items. However, since great-tailed grackles are an urban adapted species across the range, it's possible that human sources of food will not change. In particular, our middle study population in Arizona is located in the Sonoran desert, where water is scarce in natural habitats. Great-tailed grackles are a tropical species, and are likely only able to persist in the desert after humans modified the landscape by building canals and other methods of irrigation (Wehtje 2003). When expanding into and through the desert, grackles would have to adapt to the arid temperature, find new sources of water, and exploit novel biotic and abiotic food items. Secondly, as grackles expand their range north, the winter climate

becomes much more harsh. To deal with the colder northern winters, the first grackles to colonize these places were migratory (Wehtje 2003, Johnson and Peer 2001). However, after occupying these northern environments for less than 10 years, grackles apparently adapted to the cold and became non-migratory. Wehtje (2003) hypothesizes that grackles are able to expand north and survive the winter because of a concurrent expansion in large feedlots for cattle, which provide a source of grain for grackles to subsist on during the winter.

We have updated the background information in the ABSTRACT of the preregistration to include these details: “Behavioral flexibility was likely necessary for this species to adapt to novel environments during the range expansion. For example, as a tropical species, great-tailed grackles were likely only able to expand through, and persist in, the desert of the southwest United States after humans modified the landscape by building canals and other methods of irrigation (@wehtje2003range). Although grackles continue to be associated with similarly urban habitats across the range and use human-provided sources of food, one challenge grackles may have to overcome in these novel environments is gaining the ability to recognize and exploit the new stimuli that indicate natural sources of food and water. Similarly, grackles may only be able to survive the harsh winters in the most northern parts of the current range, when invertebrate prey are more scarce, because large sources of grain from cattle feedlots have become more common (@wehtje2003range).”*

Comment 7: In parts I find the methods section is lacking in detail. I find the definition of group quite vague; “a group is defined as having the same trained demonstrator(s) in the presence of many of the same conspecifics” – what constitutes ‘many’ and are you confident that enough of the same individuals will be present across multiple sessions?

*Response 7: Since we began color marking grackles in Arizona in January 2018, we continue to see ~90% of the birds we’ve caught. Additionally, the grackles seem to exhibit some site fidelity where they are most often resighted close to the location where they were originally caught, or last seen. This was also Logan’s experience of the previously studied Santa Barbara, California population. For these reasons we are confident that we will see most of the same individuals in

each group across multiple sessions. For trapping and additional research experiments (http://corinalogan.com/Preregistrations/g_exploration.html), we use food to attract grackles to an area. For these activities, we can usually attract grackles in groups of 3 - 15. Prior to the learning mechanism experiment, we will prepare grackle groups in a target area by continuously providing a source of food in the location where we will put out the apparatuses. In this way, we can train grackles to know they can dependably come to this area for food, and we will be more likely to increase group sizes. Based on the number of grackles that have overlapping home ranges in our target experimental areas, and the average group sizes that we see around our study area, we believe we will have group sizes of at least 8.

We have updated the METHODS > Planned sample section to include more information about great-tailed grackle group dynamics, and how we will prepare our learning mechanism experimental groups: “Great-tailed grackles are caught in the wild in Tempe, Arizona USA and at two additional field sites in future years (core and edge populations) for individual identification (colored leg bands in unique combinations) until as much of the population is banded as possible (62 have been marked in Tempe as of 17 Sept 2019). Great-tailed grackles are a highly social species that roosts together at night and forages in groups during the day during the non-breeding season, while during the breeding season one or more males defend a territory with multiple nests built by females who care for young (@johnson2001great). Based on our current trapping efforts in Arizona, many grackles have overlapping home ranges and when a large, temporary source of food is available, grackles will gather in groups of 3 - 15 birds. Additionally, there is some site-fidelity where the same individuals can be reliably found in the area close to where they were caught. Some individuals (~6-16) will be brought temporarily into aviaries where they will be trained on a particular locus of the apparatus. After a maximum of 6 months, these individuals will be released back to the wild to serve as demonstrators for the experiment, which will occur in the wild (in the same way as @logan2016new, except in the wild). We will attempt to train grackles in the aviaries on one solving method per bird, per apparatus, for the two visually distinct but functionally similar apparatuses (@logan2016new, @mccune*2018). However, if the solving methods on one apparatus are too*

*difficult for the aviary grackles to learn quickly, then we will only use the easier apparatus for the experiment in the wild and we will not test H3. We will conduct the social learning experiments in an area where the home ranges of many color-marked grackles overlaps. We will encourage continued attendance to this area by pre-baiting it every day for several weeks. Based on previous trapping efforts, and experiments described elsewhere (i.e. http://corinalogan.com/Preregistrations/g*exploration.html), we believe we will have learning mechanism group sizes of approximately 8 color-marked grackles."*

Comment 8: I also believe this is why a 'study species' section in the methods would be beneficial; what is the grackles social system? Do they live in stable groups? As someone who is not familiar with this study system, the suitability of it is unclear.

Response 8: Please see response 7 above, in which we included more information about our study species in the paragraphs we added to the Planned sample section.

Comment 9: I also think more information in the text is needed on each of the solving techniques, rather than trying to infer from Fig. 1.

Response 9: This is good advice! To explain each of the possible solving techniques, we've added a new section to METHODS called "Task design": "We will use two functionally similar, but visually distinct apparatuses (Fig. 1) to test social learning in this species. The first apparatus is a log that has 4 compartments (loci) covered by transparent doors that open in different ways (@mccune_2018). The top door opens up like a hatch, the left side door opens out like a car door, the front door pulls out like a drawer, and the right side door pushes in. Three of the 4 doors also have locks to increase the difficulty of the task. The lock on top is a stick that can be pushed or pulled to unblock the door, the lock on the left side is a stick that swivels up or down over the door, and the lock on the front is a hook-and-eye style lock that attaches to the handle to hold the drawer in place. The second apparatus has three loci for accessing food (@logan2016new). One locus has two methods for accessing the same food compartment, giving a total of four different options for solving the task (Fig. 1). The food in the compartment at locus 1 can be

accessed by pushing a swiveling door from the left to the right and putting the bill in the food compartment ('Vflap' option) or by pushing the same swiveling door from the right to the left and poking the bill through a piece of rubber to access the same food compartment ('Vrubber' option). At locus 2, food can be obtained by lifting up a wooden flap ('Hflap' option) to expose the compartment. At locus 3, food is obtained by inserting the bill through a hole in the side of the apparatus ('Hside' option) that accessed the same food compartment as Hflap."

Comment 10: An alternative to P2 could be a 'necessity drives innovation' mechanism, whereby subordinates outperform dominants (similar to what has been found in meerkats on problem-solving tasks).

Response 10: This is a great point, and is supported by social learning experiments in other species, like Mexican jays. We've added a P2 alternative 1 as follows: "P2 alternative 1: Subordinate individuals are more likely to solve the puzzle box faster because they are excluded by dominant individuals from other, easier to access food sources or dominants are able to scrounge from subordinates after they access the food compartments (@mccormack2007producer)."

Comment 11: How many demonstrators will there be per group?

*Response 11: We will have a minimum of one demonstrator per group. This experiment involves an open-diffusion design with wild birds, so any individual that interacts with a solving option and obtains food (or not) will also become a demonstrator. Therefore, the role of the trained demonstrators is more to ensure that there are already birds in each group who are willing to approach and start showing the others how to solve it, and to make sure that at least one solving methods is demonstrated to each group.

We updated the METHODS > Task design section to incorporate a paragraph detailing this information as follows: "Each group will have at least one demonstrator trained to open a locus on one of the two apparatuses. This experiment involves an open-diffusion design with wild birds, so any individual that interacts with a solving option will automatically become a demonstrator. Our open-diffusion analysis accounts for this by examining not only who solved

(or attempted to solve) which option, but also who was watching them solve or attempt to solve, and then measures the change in behavior of the observer."*

Comment 12: How confident can you be that observers from each group will not be exposed to other demonstrators using different opening methods? (particularly if you are unsure which birds will be at which group).

Response 12: Grackles are only given access to the apparatuses during social learning trials, and we track the presence of all color-marked individuals in a 10m area around the apparatus during each trial. Our data collection consists of quantifying the number of interactions a color-marked individual has with the apparatus. Additionally, we quantify the number of times each color-marked individual OBSERVES other grackles in the group interact with the apparatus (and we note whether the interactions they observed were successful). Therefore, we will know very specifically what each grackle sees and knows about the opening methods for each apparatus and when it acquired that knowledge. As a result, we can analyze the time to first interaction with each locus and the time to first successful opening of a locus on the apparatus as a function of the number of times the focal individual observed other grackles interacting with the apparatus. Because we are conducting an open-diffusion experiment in the wild, it is likely that naive grackles will innovate solutions to loci on the apparatus and become demonstrators themselves. Therefore, it does not matter if observers are exposed to demonstrators using other opening methods because using our analyses, all individuals become demonstrators if they interact with the apparatus. We train demonstrators in the aviaries as a way to ensure that at least one grackle will be able to open a locus on the apparatus in each group. We added text addressing this point in response to Comment 11 in the Task Design section.

Comment 13: Do you have an indication for the number of birds per group? I realise this is difficult considering group size may fluctuate, and you may not have completed banding. But it will be informative in terms of assessing the power of analyses for the core and edge sites where you only have one group at each.

Response 13: Please see our response to comment 7. You are right that this will depend on the number of color-marked birds we have in each target area by the time of the start of the social learning experiment. However, with our current frequency of trapping and the average group sizes of grackles that we see around our study area, we believe we will have groups of approximately 8 color-marked birds.

Comment 14: Presumably you will record the trials? What software will you use to score the trials?

Response 14: Thanks for bringing this up, it is definitely something we should mention! We added to the METHODS > Task Design section: "All trials will be video recorded from multiple angles or by using a camera with a fisheye lens to ensure that we can see all loci on both apparatuses and identify all of the observers. All data will be collected from scoring the videos."

Comment 15: Thank you for the interesting submission!

Response 15: We are glad you found it interesting! Thank you again for the constructive criticisms and suggestions!