



## Understanding geographic range expansions in human-dominated landscapes: does behavioral flexibility modulate flexibility in foraging and social behavior?

Open Access

Julia Astegiano and Esther Sebastián González  
based on reviews by Pizza Ka Yee Chow and Esther Sebastián González

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A recommendation of:

Corina Logan, Luisa Bergeron, Carolyn Rowney, Kelsey McCune, Dieter Lukas. **Is behavioral flexibility related to foraging and social behavior in a rapidly expanding species? (2019).** *In Principle Recommendation by Peer Community In Ecology.*

[http://corinalogan.com/Preregistrations/g\\_flexforaging.html](http://corinalogan.com/Preregistrations/g_flexforaging.html)

*Submitted: 23 October 2018, Recommended: 04 August 2019*

**Cite this recommendation as:**

Julia Astegiano and Esther Sebastián González (2019) Understanding geographic range expansions in human-dominated landscapes: does behavioral flexibility modulate flexibility in foraging and social behavior?. *Peer Community in Ecology*, 100026.

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Which biological traits modulate species distribution has historically been and still is one of the core questions of the

macroecology and biogeography agenda [1, 2]. As most of the Earth surface has been modified by human activities [3] understanding the strategies that allow species to inhabit human-dominated landscapes will be key to explain species geographic distribution in the Anthropocene. In this vein, Logan et al. [4] are working on a long-term and integrative project aimed to investigate how great-tailed grackles rapidly expanded their geographic range into North America [4]. Particularly, they want to determine which is the role of behavioral flexibility, i.e. an individual's ability to modify its behavior when circumstances change based on learning from previous experience [5], in rapid geographic range expansions. The authors are already working in a set of complementary questions described in pre-registrations that have already been recommended at PCI Ecology: (1) Do individuals with greater behavioral flexibility rely more on causal cognition [6]? (2) Which are the mechanisms that lead to behavioral flexibility [7]? (3) Does the manipulation of behavioral flexibility affect exploration, but not boldness, persistence, or motor diversity [8]? (4) Can context changes improve behavioral flexibility [9]? In this new pre-registration, they aim to determine whether the more behaviorally flexible individuals have more flexible foraging behaviors (i.e. use a wider variety of foraging techniques in the wild and eat a larger number of different foods), habitat use (i.e. higher microhabitat richness) and social relationships (i.e., are more likely to have a greater number of bonds or stronger bonds with other individuals; [4]). The project is ambitious, combining both the experimental characterization of individuals' behavioral flexibility and the field characterization of the foraging and social behavior of those individuals and of wild ones. The current great-tailed grackles project will be highly relevant to understand rapid geographic range expansions in a changing world. In this vein, this pre-registration will particularly help to go one step further in our understanding of behavioral flexibility as a determinant of species geographic distribution. Logan et al. [4] pre-registration is very well designed, main and alternative hypotheses have been thought and written and methods are presented in a very detailed way, which includes the R codes that authors will use in their analyses. Authors have answered in a very detailed way each comment that reviewers have pointed out and modified the pre-registration accordingly,

which we consider highly improved the quality of this work. That is why we strongly recommend this pre-registration and look forward to see the results.

## References

- [1] Gaston K. J. (2003) The structure and dynamics of geographic ranges. Oxford series in Ecology and Evolution. Oxford University Press, New York. [2] Castro-Insua, A., Gómez-Rodríguez, C., Svenning, J.C., and Baselga, A. (2018) A new macroecological pattern: The latitudinal gradient in species range shape. *Global ecology and biogeography*, 27(3), 357-367. doi: [10.1111/geb.12702](https://doi.org/10.1111/geb.12702) [3] Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., et al. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520(7545), 45–50. doi: [10.1038/nature14324](https://doi.org/10.1038/nature14324) [4] Logan CJ, McCune K, Bergeron L, Folsom M, Lukas D. (2019). Is behavioral flexibility related to foraging and social behavior in a rapidly expanding species? In principle recommendation by Peer Community In Ecology. [http://corinalogan.com/Preregistrations/g\\_flexforaging.html](http://corinalogan.com/Preregistrations/g_flexforaging.html) [5] Mikhalevich, I., Powell, R., and Logan, C. (2017). Is Behavioural Flexibility Evidence of Cognitive Complexity? *How Evolution Can Inform Comparative Cognition. Interface Focus* 7: 20160121. doi: [10.1098/rsfs.2016.0121](https://doi.org/10.1098/rsfs.2016.0121). [6] Fronhofer, E. (2019) From cognition to range dynamics: advancing our understanding of macroecological patterns. *Peer Community in Ecology*, 100014. doi: [10.24072/pci.ecology.100014](https://doi.org/10.24072/pci.ecology.100014) [7] Vogel, E. (2019) Adapting to a changing environment: advancing our understanding of the mechanisms that lead to behavioral flexibility. *Peer Community in Ecology*, 100016. doi: [10.24072/pci.ecology.100016](https://doi.org/10.24072/pci.ecology.100016) [8] Van Cleve, J. (2019) Probing behaviors correlated with behavioral flexibility. *Peer Community in Ecology*, 100020. doi: [10.24072/pci.ecology.100020](https://doi.org/10.24072/pci.ecology.100020) [9] Coulon, A. (2019) Can context changes improve behavioral flexibility? Towards a better understanding of species adaptability to environmental changes. *Peer Community in Ecology*, 100019. doi: [10.24072/pci.ecology.100019](https://doi.org/10.24072/pci.ecology.100019)

## Revision round #2

2019-07-01

Dear Corina and co-authors,

Many thanks for sending this revised version of your pre-registration. The two reviewers and I found that such version is highly improved and that you did a great job on clarifying many of the points that we highlighted. We appreciate your dedication and effort to improve your pre-registration and to answer our comments. Reviewer 2 has still some concerns about your predictions and the way you will measure your response variables associated with social behaviour (see below). Dr. Sebastián-González just pointed out minor comments. I agree with all comments.

Please, try to assess the points that were highlighted and provide a rebuttal letter explaining your decisions.

Best

Julia

My specific minor comments 1. Abstract. I found that your abstract is highly improved. Many thanks four your job! 2. About the populations you choose. Many thanks for providing such detailed information about the discussions you had related to this point. Now I have more elements to evaluate your design (time and financial limitations, permissions) I think that the one you are proposing is the most adequate. I particularly found interesting your partial solution (running a flexibility/individual differences test on groups of unmarked grackles at additional sites, which could really help with the issue that you bring up). 3. Species ecology. Thanks for adding so detailed information about previous knowledge on the species. 4. Social network analyses. Thank you for clarifying your analyses.

Reviewer 1 This is my second review of the pre-registration by Dr. Logan et al. This is a much-improved version of the project where most of my concerns and especially my questions on the fieldwork of the study have been addressed. I think the project is highly relevant and that it will help to go one step further in the understanding of behavioral flexibility. This pre-registration is very well designed, it has been thought and written with care and many details have been

already taken care of. For example, authors include the R code they will use in their analyses, which is very advisable. The project is ambitious, combining both experimental and fieldwork data gathering, but seems overall feasible. I only have some minor suggestions to improve clarity in the text. I am looking forward to see the results of this study! Minor comments:

- In the second sentence of H1, you use “they” to refer to the grackles (“where they must learn...”). I suggest using directly grackles to make this clear. Same in the first sentence of P3 (“the proportion of their diet”).
- The first 7 sentences of H1 are written in a confusing way, with a lot of information in bracket and a continuation of the sentence that starts in line 1 only in line 5. I suggest dividing this in two sentences.
- In methods, P4 you first cite the “strength of the maximum bond” which will be calculated as the “half-weighted index”, however, it is not until the analyses section when you explain this in detail. I suggest either moving the description of how this will be measured here, or to cite that this explanation is located in the analyses section of the proposal.
- When you explain the Independent variables for P1-P4 and P6, you cite the “Dominance rank”. In your response you say that you describe how you measure “dominance”, but not what you mean with “dominance rank” Is this just the rank of the species ordered by dominance? If so, maybe it is good to explicitly say as other may get confused such as me.

Reviewer 2 (Dr. Esther Sebastián-González) Here, I have reviewed a revised pre-registration manuscript title ‘Is behavioural flexibility related to foraging and social behaviour in a rapidly expanding species?’. I reviewed this pre-registration previously. I have to admit that I find this revision is in a much better shape than the previous version (great job!). Authors have addressed each comment in details – thank you for doing this! Overall, I still find experimentally inducing varied level of behavioural flexibility interesting. Here are some comments authors may want to take into consideration during their final revision/write up:

- 1) P1 alternative 2: if this prediction turns out to be true, it would be interesting to analyse the type of food. In particular, the contents of the chosen food type by an individual. This may provide information about the relationship between behavioural flexibility and foraging ‘success’ (e.g. more behaviourally flexible individuals may chose particular food type that has relatively more fat, high calories etc).
- 2) In this revised version, authors have provided more ecological

information about the study species than the previous one (great job!). However, I still find the information about grackles' sociality missing – this will be related to your H2 hypothesis regarding social behaviours. While I assume grackles are social species, I prefer to read a clear statement/ fact about this species (if possible). 3) I apologise for not spotting this in the earlier version. The predictions for social bonding (both in quantity and quality) suggest that records will be taken during the out-of-breeding season. However, the examples of social behaviours that authors provide in their hypothesis suggests otherwise (i.e. data will be collected during the breeding season). I wonder whether the authors are planning to conduct observation during the breeding season? If so, would authors make similar predictions? Perhaps authors could clarify this further. From my opinion, on the one hand, taking records during the breeding season may add an additional confounding variable and complicate the understanding between behavioural flexibility and social behaviours - In this case, authors shall conduct observation during the non-breeding season. On the other hand, conducting observation during the breeding season may provide interesting data to understand the relationship between the level of behavioural flexibility and mating strategies (e.g. more flexible individuals may use several strategies to gain access to females than less flexible individuals). Perhaps authors could clarify this further, too? 5) H3 is actually an interesting hypothesis – it relates behavioural flexibility and habitats choice. The two variables, foraging choices and microhabitat types, are indeed tightly correlated. Authors shall pay particular attention when testing the hypothesis. 6) Last and a more trivial comment: In 'C. Hypothesis', using 'behavioural flexibility' would not be helpful. Perhaps adding what behavioural flexibility would relate to may be useful, for example, H1: Behavioural flexibility and foraging behaviour (or in foraging context, something alike); H2: Behavioural flexibility and social behaviour (or in social context, something alike).

*Preprint DOI:*

[https://github.com/corinalogan/grackles/blob/master/EasyToReadFiles/g\\_flexforagingForReviewers.md](https://github.com/corinalogan/grackles/blob/master/EasyToReadFiles/g_flexforagingForReviewers.md)

Reviewed by **Esther Sebastián González**, 2019-05-29 15:02

This is my second review of the pre-registration by Dr. Logan et al. This is a much-improved version of the project where most of my concerns and especially my questions on the fieldwork of the study have been addressed. I think the project is highly relevant and that it will help to go one step further in the understanding of behavioral flexibility. This pre-registration is very well designed, it has been thought and written with care and many details have been already taken care of. For example, authors include the R code they will use in their analyses, which is very advisable. The project is ambitious, combining both experimental and fieldwork data gathering, but seems overall feasible. I only have some minor suggestions to improve clarity in the text. I am looking forward to see the results of this study!

Minor comments:

- In the second sentence of H1, you use “they” to refer to the grackles (“where they must learn...”). I suggest using directly grackles to make this clear. Same in the first sentence of P3 (“the proportion of their diet”).
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Reviewed by [Pizza Ka Yee Chow](#), 2019-06-15 18:18

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1) P1 alternative 2: if this prediction turns out to be true, it would be interesting to analyse the type of food. In particular, the contents of the chosen food type by an individual. This may provide information about the relationship between behavioural flexibility and foraging 'success' (e.g. more behaviourally flexible individuals may chose particular food type that has relatively more fat, high calories etc).

2) In this revised version, authors have provided more ecological information about the study species than the previous one (great job!). However, I still find the information about grackles’ sociality missing – this will be related to your H2 hypothesis regarding social behaviours. While I assume grackles are social species, I prefer to read a clear statement/ fact about this species (if possible).

3) I apologise for not spotting this in the earlier version. The predictions for social bonding (both in quantity and quality) suggest that records will be taken during the out-of-breeding season. However, the examples of social behaviours that authors provide in their hypothesis suggests otherwise (i.e. data will be collected during the breeding season). I wonder whether the authors are planning to conduct observation during the breeding season? If so, would authors make similar predictions? Perhaps authors could clarify this further.

From my opinion, on the one hand, taking records during the breeding season may add an addition confounding variable and complicate the understanding between behavioural flexibility and social behaviours - In this case, authors shall conduct observation during the non-breeding season. On the other hand, conducting observation during the breeding season may provide interesting data



to understand the relationship between the level of behavioural flexibility and mating strategies (e.g. more flexible individuals may use several strategies to gain access to females than less flexible individuals). Perhaps authors could clarify this further, too?

5) H3 is actually an interesting hypothesis – it relates behavioural flexibility and habitats choice. The two variables, foraging choices and microhabitat types, are indeed tightly correlated. Authors shall pay particular attention when testing the hypothesis.

6) Last and a more trivial comment: In ‘C. Hypothesis’, using ‘behavioural flexibility’ would not be helpful. Perhaps adding what behavioural flexibility would relate to may be useful, for example, H1: Behavioural flexibility and foraging behaviour (or in foraging context, something alike); H2: Behavioural flexibility and social behaviour (or in social context, something alike).

### **Author's reply:**

Dear Dr.'s Astegiano, Sebastián-González, and Chow, Thank you very much for considering the revision of our preregistration! We really appreciate the time you took to do this and to give us your remaining feedback. We are also really glad you think the preregistration is much improved!

We revised our preregistration and associated files at [https://github.com/corinalogan/grackles/blob/master/EasyToReadFiles/g\\_flexforagingForReviewers.md](https://github.com/corinalogan/grackles/blob/master/EasyToReadFiles/g_flexforagingForReviewers.md), and we responded to your comments (which we numbered for clarity) below (our responses are preceded by “> Response X”).

We thank you again for helping us improve this piece of research!

All our best, Corina, Luisa, Kelsey, Melissa, and Dieter

Please NOTE the addition of a new co-author, Melissa Folsom, who joined the project in February and is now working with us full time.

Round #2

Your decision by Julia Astegiano, 2019-07-01 14:20 Manuscript: [https://github.com/corinalogan/grackles/blob/master/EasyToReadFiles/g\\_flexforagingForReviewers.md](https://github.com/corinalogan/grackles/blob/master/EasyToReadFiles/g_flexforagingForReviewers.md) version v1.5 Review of your pre-registration

Dear Corina and co-authors, Many thanks for sending this revised version of your pre-registration. The two reviewers and I found that such version is highly improved and that you did a great job on clarifying many of the points that we highlighted. We appreciate your dedication and effort to improve your pre-registration and to answer our comments. Reviewer 2 has still some concerns about your predictions and the way you will measure your response variables associated with social behaviour (see below). Dr. Sebastián-González just pointed out minor comments. I agree with all comments. Please, try to assess the points that were highlighted and provide a rebuttal letter explaining your decisions. Best Julia

COMMENT 1. My specific minor comments 1. Abstract. I found that your abstract is highly improved. Many thanks four your job! 2. About the populations you choose. Many thanks for providing such detailed information about the discussions you had related to this point. Now I have more elements to evaluate your design (time and financial limitations, permissions) I think that the one you are proposing is the most adequate. I particularly found interesting your partial solution (running a flexibility/individual differences test on groups of unmarked grackles at additional sites, which could really help with the issue that you bring up). 3. Species ecology. Thanks for adding so detailed information about previous knowledge on the species. 4. Social network analyses. Thank you for clarifying your analyses.

RESPONSE 1. We are very glad that we were able to address your great feedback!

Reviews Reviewed by Esther Sebastián González, 2019-05-29 15:02 COMMENT 2. This is my second review of the pre-registration by Dr. Logan et al. This is a much-improved version of the project where most of my concerns and especially my questions on the fieldwork of the study have been addressed. I think the project is highly relevant and that it will help to go one step further in the understanding of behavioral flexibility. This pre-registration is very well designed, it has been

thought and written with care and many details have been already taken care of. For example, authors include the R code they will use in their analyses, which is very advisable. The project is ambitious, combining both experimental and fieldwork data gathering, but seems overall feasible. I only have some minor suggestions to improve clarity in the text. I am looking forward to see the results of this study!

RESPONSE 2. We are so happy for your positive feedback! We look forward to addressing your minor suggestions below.

Minor comments: COMMENT 3. • In the second sentence of H1, you use “they” to refer to the grackles (“where they must learn...”). I suggest using directly grackles to make this clear. Same in the first sentence of P3 (“the proportion of their diet”).

RESPONSE 3. Thank you for pointing out how we can be clearer. We made both of your suggested changes.

COMMENT 4. • The first 7 sentences of H1 are written in a confusing way, with a lot of information in bracket and a continuation of the sentence that starts in line 1 only in line 5. I suggest dividing this in two sentences.

RESPONSE 4. This is a good point. We split the long sentence into two sentences.

COMMENT 5. • In methods, P4 you first cite the “strength of the maximum bond” which will be calculated as the “half-weighted index”, however, it is not until the analyses section when you explain this in detail. I suggest either moving the description of how this will be measured here, or to cite that this explanation is located in the analyses section of the proposal.

RESPONSE 5. We added a note to see the full explanation in Analysis Plan > P4.

COMMENT 6. • When you explain the Independent variables for P1-P4 and P6, you cite the “Dominance rank”. In your response you say that you describe how you measure “dominance”, but not what you mean with “dominance rank” Is this just the rank of the species ordered by dominance? If so, maybe it is good to explicitly say as other may get confused such as me.

RESPONSE 6. This is a good point. We now clarify by elaborating on this independent variable: Independent variables > P1-P4 and P6 > 5) Dominance rank: measured as the number of wins minus the number of losses, divided by the sum of wins + losses. This calculation will give each individual a dominance rank number, and we will order individuals by rank from lowest to highest to create a dominance hierarchy.

Reviewed by Pizza Ka Yee Chow, 2019-06-15 18:18 COMMENT 7. Here, I have reviewed a revised pre-registration manuscript title 'Is behavioural flexibility related to foraging and social behaviour in a rapidly expanding species?'. I reviewed this pre-registration previously. I have to admit that I find this revision is in a much better shape than the previous version (great job!). Authors have addressed each comment in details – thank you for doing this! Overall, I still find experimentally inducing varied level of behavioural flexibility interesting. Here are some comments authors may want to take into consideration during their final revision/write up:

RESPONSE 7. We are so glad you think the preregistration is improved as a result of us revising per your feedback!

COMMENT 8. 1) P1 alternative 2: if this prediction turns out to be true, it would be interesting to analyse the type of food. In particular, the contents of the chosen food type by an individual. This may provide information about the relationship between behavioural flexibility and foraging 'success' (e.g. more behaviourally flexible individuals may chose particular food type that has relatively more fat, high calories etc).

RESPONSE 8. This is a great point! Thank you so much for offering this alternative for the preregistration. We added this to P1 alternative 2: "If this prediction is supported, we will conduct an additional analysis to examine what food types the more flexible grackles eat and whether these food types are potentially more valuable (measured as having more calories)." And we made an additional analysis (Analysis Plan > P1alt2) which we will run in the event that this prediction is supported: "We will rank all food types eaten by the grackles by their caloric value, examine the food types eaten per individual and relate this to their

flexibility scores on their most recent reversal learning color tube experiment. This will allow us to see whether the more flexible individuals (faster to reverse) eat more valuable (i.e., higher calorie) food types than the less flexible individuals.”

COMMENT 9. 2) In this revised version, authors have provided more ecological information about the study species than the previous one (great job!). However, I still find the information about grackles’ sociality missing – this will be related to your H2 hypothesis regarding social behaviours. While I assume grackles are social species, I prefer to read a clear statement/ fact about this species (if possible).

RESPONSE 9. We see your point here - we gave details about male breeding behavior, but not a general statement on this species’ social life. We now added this detail: “To give an example of the types of social relationships this sexually dimorphic species engages in, they forage and roost socially (@selander1961analysis) and they have a non-faithful-female frank polygynous mating system (@johnson2000male).”

COMMENT 10. 3) I apologise for not spotting this in the earlier version. The predictions for social bonding (both in quantity and quality) suggest that records will be taken during the out-of-breeding season. However, the examples of social behaviours that authors provide in their hypothesis suggests otherwise (i.e. data will be collected during the breeding season). I wonder whether the authors are planning to conduct observation during the breeding season? If so, would authors make similar predictions? Perhaps authors could clarify this further. From my opinion, on the one hand, taking records during the breeding season may add an addition confounding variable and complicate the understanding between behavioural flexibility and social behaviours - In this case, authors shall conduct observation during the non-breeding season. On the other hand, conducting observation during the breeding season may provide interesting data to understand the relationship between the level of behavioural flexibility and mating strategies (e.g. more flexible individuals may use several strategies to gain access to females than less flexible individuals). Perhaps authors could clarify this further, too?

RESPONSE 10. No need to apologize! We see how this was confusing. We have now clarified that we conduct focal follows year-round, and, with the extra detail on their general social behavior (Response 9), we hope this makes it clearer to readers that we are considering social behavior in general, beyond just their breeding behavior. To directly address your comment, we now added that we will first check for differences in degree and strength between the breeding and non-breeding seasons. This change is copied below for your convenience. If there is no difference between the seasons, we will combine the data for subsequent analyses. If there is a difference, we will use data only from the non-breeding season. Additionally, in a separate preregistration, we examine male mating strategies as they relate to flexibility ([http://corinalogan.com/Preregistrations/g\\_withinpop.html](http://corinalogan.com/Preregistrations/g_withinpop.html)). Hypotheses > H2: “There could be varying needs for males to manage their relationships with each other in breeding and non-breeding seasons” Analysis Plan > P4: “To quantify social relationships, we will conduct at least four 10-minute focal follows on each subject spaced equally across breeding and non-breeding seasons” and “Before analyzing degree and strength, we will determine if these values differ between breeding (Apr - Aug) and non-breeding seasons (Sept - Mar) because social associations could change as a result of breeding behaviors. If there is no difference, we will combine all data for the analyses described below. If there is a difference, we will only use the non-breeding season data.”

COMMENT 11. 5) H3 is actually an interesting hypothesis – it relates behavioural flexibility and habitats choice. The two variables, foraging choices and microhabitat types, are indeed tightly correlated. Authors shall pay particular attention when testing the hypothesis.

RESPONSE 11. Thank you for bringing this up. We aim to disentangle this confound by 1) quantifying what they are eating in P3 (proportion of diet that is human food), 2) using the new analysis in P1 alternative 2 to examine food types eaten and whether the more flexible individuals are eating more valuable foods (see Response 8), and 3) we added a new Prediction 8 (and associated analysis) to directly address your comment: Hypothesis > P8 “Flexible individuals will not be associated with presence in diverse microhabitats not necessarily because they

are specialists or generalists in specific foraging strategies, but rather because they may focus on high quality resources in particular habitat types. If this prediction is supported, we will conduct an additional analysis to examine the proportion of focal follows associated with a particular microhabitat type, which will allow us to determine whether the more flexible individuals are associated with particular microhabitats more than the less flexible individuals” Analysis Plan > P8 “We will examine the proportion of focal follows associated with each microhabitat per individual and relate this to their flexibility scores on their most recent reversal learning color tube experiment. This will allow us to see whether the more flexible individuals (faster to reverse) are associated with particular microhabitats more than the less flexible individuals.”

COMMENT 12. 6) Last and a more trivial comment: In ‘C. Hypothesis’, using ‘behavioural flexibility’ would not be helpful. Perhaps adding what behavioural flexibility would relate to may be useful, for example, H1: Behavioural flexibility and foraging behaviour (or in foraging context, something alike); H2: Behavioural flexibility and social behaviour (or in social context, something alike).

RESPONSE 12. We see your point - the first sentence of each hypothesis was so long that the main message wasn’t coming through. We revised H1 based on advice from Reviewer 1 (Response 4), and we applied these changes to H2 and H3, which should address your comment here as well. H1 “Behavioral flexibility (see @mikhalevichis2017 for a detailed definition) is related to foraging behavior (measured with focal follows using this ethogram) in wild individuals (after their release from the aviaries).” H2 “Behavioral flexibility (see @mikhalevichis2017 for a detailed definition) is related to social behavior (measured year-round with focal follows using this ethogram in wild individuals.” H3 “Individuals that are behaviorally flexible (see @mikhalevichis2017 for a detailed definition) will differ in their use of microhabitats within human-modified landscapes (substrate qualification during each focal follow), but the macrohabitat (square kilometer) of each population will not differ in human population density”

## Revision round #1

2019-03-16

Dear Dr. Corina Logan and co-authors,

Thank you for submitting your preregistration “Is behavioral flexibility related to foraging and social behavior in a rapidly expanding species?” to PCI Ecology. My sincere apologies for the delay in giving you a first answer.

Dr. Esther Sebastián-González, an anonymous reviewer and myself have now reviewed your preregistration. You will find our general and specific comments below. I hope that they will help to improve your project. We all agree that this is an interesting, original and timely project. However, Dr. Sebastián González have some concerns on your hypotheses and the way you will carry out fieldwork related to the characterization of foraging and social behavior. Reviewer 2 suggests that (1) you should include general background information supporting your hypotheses, (2) reformulate your hypotheses to include the alternative predictions, and (3) rethink about how you will measure and characterize some of your variables. I agree with all their comments and suggestions, and I have some additional ones in the same line that are explained below.

I would like to invite you to submit a revised version of this pre-registration considering all comments and suggestions.

Sincerely

Julia

### General comments

About the populations you will sample My main concern is related with the design of your study. You decided to conduct your study in three populations and consider them as blocks in your statistical analyses since you recognize that different relationships among variables can be expected in each population, which I agree. However, I am not sure that the populations you chose will be the most informative for your general question concerning the role of behavior flexibility on rapid range expansion. I mean you will use one population from the



center, one from the middle and one from the edge of the geographic range of the species. If you are trying to understand the role of behavior flexibility in the expansion of a species range, why focusing on a population from the center of the species distribution and not different populations from the edge (i.e. trying to represent different edge conditions)? It is widely recognized that the different edges of the geographic range of species will impose different limitations for range expansion. Moreover, I expect geographic range expansion be more linked with populations in the edge of the geographic distribution of a given species. Then I think it will be more informative to perform your study in different populations from the edge of the geographic range of grackles, having central populations as controls.

I also suggest that you provide more information on the ecology of the species and the expansion of its range, which certainly may help understand your decisions about the populations that will be sampled.

In regard with your study design, have you thought about the possibility of comparing the association between behavioral variation and foraging and social behavior across species with contrasting geographic ranges or that expanded their range at different speeds? Have you considered performing such comparative analyses in the future?

Data analyses Social network analyses are comparatively less explained than other analyses. Please, include more information on which variables you will measure and how you will do it, how you will construct random networks and how you will compare your observed social network with randomized ones.

#### Specific comments

Abstract “However, behavioral flexibility is rarely directly tested at the individual level, thus limiting our ability to determine how it relates to other traits, which limits the power of predictions about a species' ability to adapt behavior to new environments”. This sentence is not clear to me. Which other traits? Other traits that are already know to relate to rapid geographic range expansion? What do you mean by rapid geographic range expansion? Please, try to be as specific as you are in the following sentence: “Results will allow us to determine whether (...)

individual-level variation in flexibility is linked with diet breadth, foraging proficiency, social interactions, habitat use, and movement into new geographic areas”.

“We use great-tailed grackles (a bird species) as a model to investigate this question because they have rapidly expanded their range into North America over the past 140 years ((Wehtje 2003), (Peer 2011)) (Fig. 1)”. Here I suggest you provide more information about the natural history explaining the expansion of the geographic range of this species, in order to link it with the mechanisms you are proposing to evaluate in this project. Does this rapid expansion include new biomes? Or is the species just moving on the same kind of environments (i.e. expanding more by modifying dispersal ability and not new habitat use?). Are grackles using different vegetation cover types?

“This investigation: In this piece of the long-term project, we will assess whether performance in experiments that assess behavioral flexibility relates to variation in ecological and social behavior in the natural environment”. Are you referring to individual performance and individual variation? Or is it individual performance and across-individual (population) variation in ecological and social behavior? By being more specific in the formulation of these questions you may allow readers to evaluate their match with the methodology you are proposing. From this abstract is difficult to see if you will evaluate variation in flexibility, ecological and social behavior just at the individual level.

Hypotheses “H1: Individuals that are more behaviorally flexible (measured by reversal learning and switching between options on a multi-access box) will differ in their foraging behavior in the wild (measured with focal follows)”. I suggest you rewrite your hypothesis as: Behavioral flexibility is related to/modulates/influences foraging behavior. “Prediction 1: (...) validating the cross-species correlational finding that technique breadth (Overington et al. (2009)) and diet breadth (Ducatez, Clavel, and Lefebvre (2015)) indicate flexibility”. I suggest you change “indicate” by “are associated to”.

“P1 alternative 1: If there is no correlation, this suggests that flexibility is an independent trait from the number of foods eaten and foraging techniques used.”

Why you use a statistical term in your prediction? I suggest you use “relationship” or association. On the other hand, since flexibility is the factor of analysis in fact this will suggest that the number of foods eaten and foraging techniques used are independent from behavioral flexibility.

“P1 alternative 1: (...) Flexibility is not necessarily associated with diet and foraging technique breadth because flexibility could be constrained in a foraging context due to social competition (e.g., subordinates are outcompeted while foraging and thus try new foods and techniques) or ecological limitations (e.g., constrained by what is available)”. In the same line of my previous comment and following the logic you presented previously, you should state that foraging techniques and items might be constrained by other factors such as... For me, this will constitute an alternative hypothesis and not an alternative prediction.

“P3: The more flexible individuals eat more human food, potentially due to A) having stayed in their parent's home range (i.e., they eat human food because it happens to be more prevalent in their home range than in other home ranges; local specialization) or B) because these individuals move around to seek out such opportunities (potentially seeking out habitat edges within their population). Foods eaten will be recorded during focal follows”. What does it mean “more human food”? More quantity? More items? Eating human food will be considered an expansion of their diet (i.e. adaptation to new environments) or not? How innovative techniques will function in this case? Do you have predictions on these techniques? Thinking on the populations you chose (see general comments): Do the populations that you propose to sample differ on their proximity to urban areas? How may this proximity affect the relationships you expect to find? “H3: Individuals that are more behaviorally flexible (measured by reversal learning and switching between options on a multi-access box) will use a wider range of habitats (measured with GPS point for each focal follow).” Can you be more specific about what you will consider different habitats and therefore how you will measure the range of habitats? In P5 and P6 you use diversity of habitats so I think it will help to have a more specific definition of habitat here. Will you use different vegetation cover types? Or compare wild, semi-natural and urban habitats?

METHODS P6: flexible = wider range of habitats 1. Evenness in the proportion of time spent in each habitat type (grass, gravel and other natural substrate, cement, cafe, dumpster). Comment: Why you use one measure of habitat diversity? I suggest you use different qualitative and quantitative measures to fully understand habitat use or provide a strong argument to just use evenness (which I found will provide you a highly constrained definition of habitat use).

About the use of G tests It is not clear for me why you present those G tests if (1) you cannot include the exact variance structure of your future models, which will modify the sample size you will need; (2) you are planning to use the Bayesian approach.

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Reviewed by [Esther Sebastián González](#), 2019-01-10 10:43

Dr. Logan et al have pre-registered an interesting project to study the relationship between the flexibility in the behavior of grackles and several individual characteristics such as their diet, foraging strategies and social relationships. The main novelty of this project is that it focuses on individual differences, while most previous studies have worked at population level. The hypotheses are in general well described and tailed to the methods that will be used. The authors have also provided with a very detailed description of the statistical analyses that they will perform, including the R code. I have some concerns with the methodological design and the hypotheses, as well as suggestions of improvement in the description of the variables and of the stats.

My main concern is with the fieldwork. Besides being very informative in other aspects, the pre-registration does not provide with much information about how the fieldwork will be carried out, and it is very important. For example, how will you gather the information on the diet, bonding, foraging strategies, or the probability of being an immigrant for the individuals that are in the field? Will you follow them? For the bonds analysis you indicate that “To quantify social relationships, we will conduct at least four 10-minute focal follows”, but nothing is said for the other variables. How will you do the survey for the remaining variables? Will you try to resample in different days? How likely is that you

resample one individual? I am worried that if you cannot resample the individuals enough times, that won't give you the information on their entire diet or foraging techniques used. It is also not very clear to me how will you do the behavioral test in the field, will you keep individuals until they solve a loci and then do the reverse learning test? It looks to me that some of the hypotheses can be only tested with aviary individuals while others with field individuals, or with both of them. It will help to understand how you will perform the study if you include the information on what group of individuals you will use to test each prediction. It may be that this is well explained in another pre-submission, but it would be nice to have it here a bit more detailed. Finally, are you planning to compare the behavior of the individuals that have been in the aviary for some time with those that won't? It looks like you will measure both. I think it would be very interesting at least to compare the diet, bonding and foraging techniques among them to be sure that being in the aviary is not affecting them. Or maybe this can be an additional predictor variable to be included in your analyses.

I also have some comments for some of your hypotheses: P3: You can easily test hypothesis P3 A) if you do a fast estimation of the amount of food available in the surroundings of your observation and compare how frequent human food is and how frequent it is consumed by the species. Additionally, I can also think about a P3 C) the more flexible individuals eat more human food because they have the foraging techniques required to consume those new food items.

In P3 alternative A, I'd complete the sentence specifying that "their daily range sizes encompass many different food resources, including human foods, but they are not specialized on them". Also, I think that if P3 alternative B happens, then the correlation between an individual's flexibility and the amount of human food in their diet would be negative.

I had to read P4 alternative 1 a couple of times to fully understand it due to the negative on it. I think it would be easier to read if you change it to something like "Individual flexibility is not related to having stronger bonds..."

I also think it would help the reader to see a short description on how you will calculate the following variables, as you do with the others: 1. Relatedness for the strongest bond 2. Probability of being an immigrant 3. Dominance rank

In the “analysis” sections there is a lot of repetition about how you will perform the GLMMs and the Power analysis. This is a matter of taste, but the sections of the description that are the same can potentially refer to the first time written and avoid repetition. Alternatively, you can write a section about the models and the power analysis and refer to it while describing the analyses for each hypothesis and prediction.

In the section “P4: flexible = stronger bonds” I have a couple of things to say: First, I am not sure about how you will create the social network. If you plan to use field data, you will not be able to identify all the individuals, as many of them will not be banded. If you use the data from the aviary, you will be sampling a very reduced “community”, unless you have a huge aviary to do the study. Also, you describe the power analysis and then say that tit is the same than in P1-P2, so maybe you can exclude the description from here. In the last paragraph of the section P4: flexible = stronger bonds there is a missing reference also, written as (???).

Reviewed by [Pizza Ka Yee Chow](#), 2019-03-08 05:05

Here, I have reviewed the preregistered manuscript title ‘Is behavioural flexibility related to foraging and social behaviour in a rapidly expanding species’ by Logan and colleagues. Overall, I think this is a timely and interesting study that can contribute to the understanding about the evolution of behavioural flexibility. I do find the manipulation of flexibility experience particularly interesting! While I am happy with the overall presentation of the manuscript (as a pre-registered standard), I do have some comments/suggestions which hope the authors would address them in their final submission.

Missing general background information. Although I know this is a pre-registered manuscript, I would appreciate if authors would provide a brief background information about how hypotheses/ predictions are formed; it is a bit awkward

when authors just provided information about more behaviourally flexible birds would differ in their foraging behaviours right at the beginning of the document... A similar comment for the methods; a brief information about what is reversal learning or what the multi-access box is like (at least how many solutions are there??) would be helpful to understand how authors would like to examine flexibility (as opposed to clicking a link that actually related to another registration). For example, what indicate flexibility in literature; 'faster' to reverse preference in reversal learning is measured as the total number of choices/the number or errors/the number of correct choices that a grackle made before reaching a learning criterion?

Hypotheses should be presented in a general sense (e.g. 'the level of flexibility in individual would be correlated with their foraging behaviour in the wild') so as to cover different directions of predictions.

Additional point to consider: 1) In hypothesis one, if there is no correlation between the flexibility of reversal learning and the number of food consumed or the number of types of habitats used, do authors really think the results are reflecting independent traits? Or both are under the umbrella term of 'flexibility' but reflecting a different 'form' of flexibility? likewise for P1 alternative 2 and alternative 3: would the negative correlation actually help to reflect these flexible behaviours are different 'forms' of flexibility? 2) Hypothesis 1 P2- Have authors thought of how quick would the birds learn not to eat certain food as a measure of flexibility too? That said this may not be ethically manipulated through experiments... 3) Hypothesis 2. Social bonding may not only be assessed in quality but also quantity – the number of 'buddies' they interact with rather than being 'best friends' with everyone. 4) P4 alternative 2 – 'because they frequently change their behaviour and are difficult to form bonds with' - This needs to be measured properly because the change of behaviour is also a form of flexibility though not in social context. 5) P6 alternative – it would also well be individuals prefer certain type(s) of habitats after initial exploration. If this is the case, authors may have to limit or quantify the use of different types of habitats at the initial stage.

Independent variables: 1) Flexibility 2. 'no choice' trials are a good way to control the confounding factor 'exploration'. But the independent variable should focus on what the ratio really represents – how do correct and incorrect choices really relate to flexibility? 2) Authors are right to predict that the number of trials to reach a learning criterion in the reversal phase may not necessarily relate to the latency of solve new loci on the multi-access box. But have authors also considered using the number of experience that requires a bird to reach asymptotic performance in the multi-access box as an indicator of flexibility? This is because both are measuring flexibility after a change occurs.

### **Author's reply:**

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