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Explore and move: a key to success in a changing world

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Explore and move: a key to success in a changing world?

Blandine Doligez based on reviews by *Laure Cauchard, Marion Nicolaus and Joe Nocera*

A recommendation of:

Kelsey B. McCune, Cody Ross, Melissa Folsom, Luisa Bergeron, Corina Logan. **Does space use behavior relate to exploration in a species that is rapidly expanding its geographic range?** (2020), *In Principle Recommendation. PCI Ecology*. <http://corinalogan.com/Preregistrations/gspaceuse.html> version 23 Sep 2020

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Changes in the spatial range of many species are one of the major consequences of the profound alteration of environmental conditions due to human activities. Some species expand, sometimes spectacularly during invasions; others decline; some shift. Because these changes result in local biodiversity loss (whether local species go extinct or are replaced by colonizing ones), understanding the factors driving spatial range dynamics appears crucial to predict biodiversity dynamics. Identifying the factors that shape individual movement is a main step towards such understanding. The study described in this preregistration (McCune et al. 2020) falls within this context by testing possible links between individual exploration behaviour and movements related to daily space use in an avian study model currently rapidly expanding, the great-tailed grackle (*Quiscalus mexicanus*).

Movement and exploration: which direction(s) for the link between exploration and dispersal?

Individuals are known to differ in their tendency to explore the environment (Réale et al. 2007; Wolf and Weissing 2012) and therefore in their motivation to move. Accordingly, exploration has been shown to relate to dispersal behaviour, i.e. movements between breeding sites (Dingemanse et al. 2003, Le Galliard et al. 2011, Rasmussen and Belk 2012; reviews in Cote et al. 2010, Ronce et al. 2012). Yet, the mechanisms underlying this link often remain unclear, due to the correlative nature of the data. A classical assumption is that dispersers may benefit from a high capacity to explore, allowing them to familiarize quicker with their new environment once reached, thus alleviating dispersal costs (Bonte et al. 2012). The association between dispersal and exploration would in this case result from selection for this combination of traits (Ronce et al. 2012), even though dispersal event itself may be independent from (and precede the effect of) exploration behaviour. Alternatively (but not exclusively), dispersal may simply be the final outcome of longer

movements by individuals exploring larger ranges (Badyaev et al. 1996, Schliehe-Diecks et al. 2012). In the absence of easy ways to manipulate dispersal behaviour, on the one hand, and exploration tendency, on the other hand, investigating detailed, small-scale individual movements in relation to exploration should thus shed light on which processes may yield the observed relations between exploration as an individual personality trait and large-scale, long-term movements, such as dispersal, underlying species range dynamics. In this project, the exploration behaviour of grackles will be measured in controlled conditions using standardized tests in captivity (McCune et al. 2019) before individuals are released and their daily space use behaviour will then be measured using remote tracking over long time periods (McCune et al. 2020). Importantly, these coupled measures will be obtained for individuals captured in three different populations: within the historical range of the species, in the middle of its expanding range and at the edge of the range (McCune et al. 2020). Therefore, the project will test (i) whether daily space use of individuals is linked to their intrinsic exploration tendency and (ii) whether space use differs between individuals from different populations along the expanding range. The preregistration echoes a complementary project by the same team that will focus on exploration and test (iii) whether exploration tendency differs between individuals from these different populations. Taken together, these three analyses will therefore provide solid background information to assess the role of exploration in the individuals' decisions leading to movement and range dynamics in this species. As underlined in the preregistration, previous studies addressing the links between individual exploration behaviour and movements have mostly focused on dispersal. A first type of studies have (as will be done here) measured exploration behaviour of individuals, often in captivity (Dingemanse et al. 2003, Korsten et al. 2013) but also in the wild (Rasmussen and Belk 2012, Debeffe et al. 2013), and related these measures to subsequent dispersal behaviour. The (often implicit) underlying assumption is that more exploratory individuals will be more likely to move further, explore different habitats and thus end up breeding farther than less explorative ones. In other words, exploration tendency precedes and drives dispersal. Sometimes, exploratory behaviour is measured on individuals of known dispersal status, i.e. after the dispersal event (Hoset et al. 2011), in which case selection for certain exploration phenotypes among dispersers may already have occurred. Besides this first approach, another type of studies have measured 'exploration' behaviour under the form of prospecting movements of individuals and linked these movements to subsequent dispersal (often in the context of habitat selection). While these studies were in the past based on direct thus potentially biased observations (Reed et al. 1999), they now rely more and more on technological advances using (miniaturized) remote tracking devices (Ponchon et al. 2013) that provide far more complete and unbiased movement data, and sometimes also complementary measures of individuals' internal state. In this case, the implicit assumption is that individuals prospecting farther and/or in more habitat patches will be more likely to settle in a site located farther away from their departure site, because of a more exhaustive sampling of possible sites allowing individuals to identify higher-quality sites (Badyaev et al. 1996). In other words, exploration tendency would not directly lead to higher movements or longer distances, but would allow individuals to optimize their habitat choice among more numerous options, thus leading to an increased dispersal probability or distance; the relation between exploration and dispersal would thus be indirect. Prospecting studies address more closely the underlying mechanisms of movement; however, they cannot easily separate intrinsic individual exploratory tendency from the prospecting movements themselves, with potential feedback effects of the information already gathered on future exploration of other sites or patches, thus on subsequent movements. By focusing on individual daily space use movements as a mechanistic approach to understand large-scale movements potentially involved in colonization and range expansion, the grackle study described in this preregistration (McCune et al. 2020) will thus contribute to bridge the knowledge gaps between exploration and dispersal. By linking exploration measures obtained from a battery of standardized tests conducted in controlled conditions to individual daily space use and movements recorded in the wild, the grackle project is set in between previous studies addressing the links between exploration and dispersal: it will document exploration in a separate and independent context with respect to the movements themselves, and it will use a mechanistic view of detailed movements by the same individuals in the wild to explore potential implications for dispersal and range expansion. Testing differences between the three study populations over the species range will indeed inform about potential large-scale, population implications of among-individual

variation in the link between exploration and movements. Because this study will only measure already settled adult individuals whose previous history is unknown, there will nevertheless be no direct possible exploration of the link with either previous or subsequent dispersal behaviour. Thus, the potential links studied here relate more directly to post-dispersal benefits of exploration for an optimal exploitation of the new environment. Yet, if exploration is a life-long personality trait linked to daily movement patterns, it may also relate to natal dispersal movements in young individuals.

Evolutionary and conservation perspectives

If the results of the project reveal that exploration tendency and daily space use movements are indeed linked, and that individuals from populations across the species range differ in these traits, new questions will emerge. A first question would be whether such among-individual differences are at the origin of range expansion or rather one of its consequences since, again, we deal with correlative data here. In other words, individuals may differ in exploration tendency, and this may confer them different ability to move around, find and colonize new habitats; or individuals may show differences in exploration following arrival in a new habitat, either because more explorative individuals gain fitness benefits and are thus selected, or because of behavioural plasticity and post-colonization adjustment of exploration behaviour when facing new ecological and social conditions in the new environment. Another open question relates to the link between daily space use and dispersal: is dispersal a by-product of higher daily movements that allow individuals to discover new favorable places where to settle? Exploring this link could involve measuring just fledged individuals before natal dispersal occurs and/or individuals chosen according to their own dispersal history, and this would then imply long-term population monitoring as an efficient (but constraining) tool to address such questions. Finally, assessing the fitness consequences of the link between exploration and space use behaviour, and whether these consequences differ between populations along the range expansion, would also be needed to understand the contribution of this link to the invasion success of this species. The study model chosen for this project is a rapidly expanding species. Importantly, however, and as emphasized in the preregistration, documenting links between exploration and daily space use patterns as well as differences between populations with different trajectories can provide crucial information in general to understand population persistence in response to global climate and landscape changes, both regarding invasion ability or extinction risk. The information should be key to assess the probability that a species may decline, persist or expand in studies addressing biodiversity and community dynamics in a changing world.

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Revision round #4

2020-09-17

Dear authors,

Thank you very much for the changes made in the manuscript, especially in the introduction section to put the focus on the biological context of the study rather than on the methods. To me, it is now as close as possible to the introduction of a “standard” paper. I understand the authors’ willingness for not changing this introduction a posteriori in the future resulting publication, and to me this introduction now presents the rationale of the study very well (including the presentation of the study model in view of reporting results before detailing methods as planned). Well done!

I am of course ready to recommend the preregistration, but as I understood that all changes need to be done at this stage, there is still one point that requires checking in the current version of the text: I spotted in the introduction three occurrences of “???” where there should be references (in the first, second and last paragraphs). Can you please check these out to make sure that the corresponding references appear correctly?

In addition, because you intend to keep the introduction as it currently is for later reporting of the full study, I have a few other small suggestions to still improve the clarity of this section (I hope you will not find those remarks too picky!):

- “Range expansions leading to problematic invasive species are occurring across the globe”: maybe reformulate here to “Problematic range expansions of invasive species are occurring across the globe” or “Range expansions leading to problematic invasions are occurring across the globe”
- “Within-species variation in the ability (movement) and motivation (exploratory tendency) to encounter conspecifics, novel foods, and novel food sources could be a limiting factor in successful species range expansions”: is it really within-species variation that is a limiting factor? Or rather limited ability and motivation to move themselves? Within-species variation should on the contrary favor such expansion (the higher the within-species variation, the higher the chances that some individuals with extreme phenotypes may successfully settle in new places)
- “the occurrence of conspecifics, food, and predators”: but also heterospecific competitors, parasites... maybe the list should remain open for the many environmental factors concerned a priori
- “Additionally, common mynas were faster to approach a novel object for food in urban areas where novelty is frequently encountered compared with mynas in areas with low exposure to novelty”: sorry I do not clearly see the link with the preceding idea here about differences between core and edge habitats as the focus is here mostly on between-individual differences rather than between habitat differences. Can you please rephrase here? (e.g. start with urban areas imposing high level of novelty, thus favoring more explorative individuals (here mynas) compared to rural areas, as a second example here?)
- “while dispersal has been shown to vary based on exploratory tendency”: consider replacing by “while dispersal and exploratory tendencies have been shown to be associated” because these are only correlations, not causal relations (in most cases at least – I can recall only one selection experiment on exploration in great tits that drove longer dispersal distances, if I remember well – but I could not find again the reference!)
- “Space use behavior is influenced by internal states like exploratory tendency and hunger”: maybe replace by “Space use behavior is expected to be influenced by internal states like exploratory tendency and hunger” otherwise you would already state as certain what you plan to investigate here?
- Maybe consider being more general in the following sentence by adding this suggested part: “Instead, spatial and temporal autocorrelation, where the position of an individual at a given time will be tightly linked to its position both before and after, including cases where individuals are repeatedly found in the same locations across time”
- Consider a slight change: “The nature and level of ecological and social factors grackles experience may vary in importance between populations...”
- Typo: “TGenerally, this species is strongly...” (remove T)
- Consider slight changes: “First, we will test whether grackles’ performance on exploration tasks in captivity is related to the space use metrics of the same individuals ...”

Preprint DOI: <http://corinalogan.com/Preregistrations/gspaceuse.html>

Author's reply:

Dear Dr.'s Blandine Doligez, Joe Nocera, Marion Nicolaus, and Laure Cauchard, Thank you for the follow-up comments! We have incorporated your edits as described below. We revised our preregistration and associated files at <http://corinalogan.com/Preregistrations/gspaceuse.html>, and we responded to your comments below. Note that the version-tracked version of this preregistration is in markdown at GitHub: <https://github.com/corinalogan/grackles/blob/master/Files/Preregistrations/gspaceuse.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 has been further improved due to additional feedback! All our best, Kelsey, Cody, Melissa, Luisa, and Corina

Does space use behavior relate to exploration in a species that is rapidly expanding its geographic range?

Kelsey B. McCune, Cody Ross, Melissa Folsom, Luisa Bergeron, Corina Logan

Recommender: Blandine Doligez

Comment 1: Dear authors, Thank you very much for the changes made in the manuscript, especially in the introduction section to put the focus on the biological context of the study rather than on the methods. To me, it is now as close as possible to the introduction of a “standard” paper. I understand the authors’ willingness for not changing this introduction a posteriori in the future resulting publication, and to me this introduction now presents the rationale of the study very well (including the presentation of the study model in view of reporting results before detailing methods as planned). Well done!

Response 1: Thank you! It has been very helpful to work with you on this preregistration.

Comment 2: I am of course ready to recommend the preregistration, but as I understood that all changes need to be done at this stage, there is still one point that requires checking in the current version of the text: I spotted in the introduction three occurrences of “???” where there should be references (in the first, second and last paragraphs). Can you please check these out to make sure that the corresponding references appear correctly?

Response 2: So sorry! We have found and fixed these citations.

Comment 3: In addition, because you intend to keep the introduction as it currently is for later reporting of the full study, I have a few other small suggestions to still improve the clarity of this section (I hope you will not find those remarks too picky!): “Range expansions leading to problematic invasive species are occurring across the globe”: maybe reformulate here to “Problematic range expansions of invasive species are occurring across the globe” or “Range expansions leading to problematic invasions are occurring across the globe”

Response 3: Your input is helpful and has improved the clarity of the introduction. We made this suggested change.

Comment 4: “Within-species variation in the ability (movement) and motivation (exploratory tendency) to encounter conspecifics, novel foods, and novel food sources could be a limiting factor in successful species range expansions”: is it really within-species variation that is a limiting factor? Or rather limited ability and motivation to move themselves? Within-species variation should on the contrary favor such expansion (the higher the within-species variation, the higher the chances that some individuals with extreme phenotypes may successfully settle in new places)

Response 4: You are right, the literature indicates that species invasions likely fail when there is little variation in the behavioral types of the pioneer individuals (Holway & Suarez 1999). When there is not a mix of behavioral types, then even individuals with an extreme exploratory phenotype (for example) might colonize an area, but not successfully breed or survive (Carere & Gherardi 2013). So the within-species variation is really what is needed in pioneers. Theoretically, individuals on an expanding edge of the range will exhibit more extreme phenotypes and variation in phenotypes (Shine et al. 2011). We have clarified this by adding content and rearranging the paragraph: “Within-species variation in the ability (movement) and motivation (exploratory tendency) to encounter conspecifics, novel foods, and novel food sources could be a limiting factor in successful species range expansions [at Spiegel2016feedback]. In novel areas, the occurrence of conspecifics, food, predators and other environmental factors may not be as easily detectable or recognizable, and may be distributed differently across the landscape than in core areas of the range. Although individuals with exploratory phenotypes may be more successful at colonizing new habitat,

exploratory individuals are also at higher risk of predation [stuber2013slow], and could be less likely to find local food sources [van2009personality]. Consequently, for establishment in new areas, individuals that exhibit a range of exploratory behavior are needed, and the interaction between space use and exploratory tendency is likely important for finding novel foods and food sources. Additionally, while dispersal [the permanent movement an individual makes from its birth site to the place where it reproduces; greenwood1982natal] is necessary to initially invade the novel habitat, subsequent daily space use could determine establishment success. For example, on the range edge conspecific density might be lower and individuals may need to use space differently [bubb2006movement]. However, current research on invasion success and movement behavior focuses heavily on dispersal, and while dispersal and exploratory tendencies have been shown to be associated [cote2010personality], we do not know how exploratory tendency influences space use patterns in the daily lives of invading individuals.”

Comment 5: “the occurrence of conspecifics, food, and predators”: but also heterospecific competitors, parasites... maybe the list should remain open for the many environmental factors concerned a priori

Response 5: Good idea. We updated this sentence to say: “...the occurrence of conspecifics, food, predators and other environmental factors...”

Comment 6: “Additionally, common mynas were faster to approach a novel object for food in urban areas where novelty is frequently encountered compared with mynas in areas with low exposure to novelty”: sorry I do not clearly see the link with the preceding idea here about differences between core and edge habitats as the focus is here mostly on between-individual differences rather than between habitat differences. Can you please rephrase here? (e.g. start with urban areas imposing high level of novelty, thus favoring more explorative individuals (here mynas) compared to rural areas, as a second example here?)

Response 6: You are right that this sentence is abrupt. We deleted this sentence during a rearrangement of this paragraph to address comment 4. Please see our Response 4 for the revised paragraph.

Comment 7: “while dispersal has been shown to vary based on exploratory tendency”: consider replacing by “while dispersal and exploratory tendencies have been shown to be associated” because these are only correlations, not causal relations (in most cases at least – I can recall only one selection experiment on exploration in great tits that drove longer dispersal distances, if I remember well – but I could not find again the reference!)

Response 7: Good point and we reworded this sentence as you suggest.

Comment 8: “Space use behavior is influenced by internal states like exploratory tendency and hunger”: maybe replace by “Space use behavior is expected to be influenced by internal states like exploratory tendency and hunger” otherwise you would already state as certain what you plan to investigate here?

Response 8: Thank you for this suggestion, we made this change.

Comment 9: Maybe consider being more general in the following sentence by adding this suggested part: “Instead, spatial and temporal autocorrelation, where the position of an individual at a given time will be tightly linked to its position both before and after, including cases where individuals are repeatedly found in the same locations across time”

Response 9: Good idea, and we incorporated your suggestion by dividing this up into separate sentences: “Spatial and temporal autocorrelation occurs when the position of an individual at a given time is tightly linked to its position both before and after, including cases where individuals are repeatedly found in the same locations across time. This autocorrelation is an intrinsic component of space use behavior and eliminating it can reduce biological relevance and obscure relationships with behavioral types [dray2010exploratory].”

Comment 10: Consider a slight change: “The nature and level of ecological and social factors grackles experience may vary in importance between populations...”

Response 10: Thank you for this edit, we made this change.

Comment 11: Typo: “TGenerally, this species is strongly...” (remove T)

Response 11: Thank you for catching this! Sorry for the oversight and we made this change.

Comment 12: Consider slight changes: “First, we will test whether grackles’ performance on exploration tasks in captivity is related to the space use metrics of the same individuals ...”

Response 12: This is a nice refinement of this sentence and we made this change.

Revision round #3

2020-09-01

Dear authors,

Thank you for your very detailed answers to our questions and comments in the last round, and in particular for adding a clear introductory section presenting the context of the study, the objectives, the general methods and potential implications. This section is currently a sort of a mix between introduction, methods and discussion as would be in a standard paper, and I think it will need to be reorganized in the manuscripts resulting from the study, but for now I am fully satisfied with this section that perfectly addresses my previous demand for a more dedicated section on presenting the study. In particular, I find the link between the individual processes and the population-level expansion question and the rationale for grouping the two main questions of interest here now much clearer; both aspects are now much better integrated (including in the title).

I am therefore happy to recommend the pre-registration for PCI Ecology, and of course wish you good luck for the continuation of the project. I list below a few more details (and a few comments) that you could consider to still improving the text before publication.

Abstract : - “Range expansion could be facilitated by individuals on the range edge that consistently differ in behavior compared to individuals in other parts of the range”: consider replacing by: “by consistent behavioural differences between individuals on the range edge and those in other parts of the range”? - “We will compare performance on an exploration task in captivity to subsequent space use behavior in the wild”: consider replacing by “we will test whether performance on an exploration task in captivity relates to subsequent space use behavior in the wild”? - add identify in “e.g. identify which individuals are likely to remain...”

Introduction: - “Duckworth and Badyaev (2007) found that the more aggressive male western bluebirds dispersed the furthest”: strictly speaking, I do not think that these authors explored dispersal distance, but they found that new individuals in a population (defined as dispersers) were more aggressive. Consider rewording here accordingly? - “thus facilitating the range expansion and displacing the less aggressive mountain bluebirds”: not sure that this is easily understandable for readers not familiar with this earlier paper, consider replacing by “thus facilitating the displacement of competing but less aggressive mountain bluebirds and favoring range expansion” or something like this? - citation for the definition of dispersal: instead of Cote et al. 2010, it would be more appropriate to cite Greenwood 1980 or 1982 - “novel foods, and food sources”: what do you mean here by distinguishing both? - consider adding the bold parts in the following sentence: “Traditional studies of animal space use required spatial and temporal independence of data points for statistical analysis (Swihart and Slade 1985). Yet, movement behavior is influenced by internal state, as well as the availability of habitat and resources, which can be distributed non-randomly across the landscape (Nathan et al. 2008), and movement data points are therefore and by construction unlikely to meet such spatio-temporal independence criteria.” (otherwise, which link do you make between these two sentences?) - the 3rd paragraph is entirely methodological and comes a bit early in the manuscript, but this

will certainly be re-adjusted in the resulting publication after the study is completed. - 4th paragraph: I personally prefer to remain general as long as possible in the introduction and detail the study species specificities only in the methods, while keeping only general aims and objectives in the introduction. But again, you will see later on whether you wish to adjust the text accordingly in the resulting manuscripts. - internal state (singular)? - “with these ecological and social factors which may vary”: add a coma after factors - first sentence of 5th paragraph: maybe make a transition here to start with (To better understand...), and I think it could be good to separate (i) the general objectives (testing the relation between exploratory tendency and space use behaviour) and (ii) the contexts for measuring these two behaviours (in captivity for exploration, in the wild for space use). This could simply be done by a slight change such as “We aim to understand whether measures of exploration, measured in captivity, are associated with space use behavior, measured in the wild, in grackles from three populations...” but importantly would place the focus back to the general objective. - consider adding the bold part in the following sentence: “measured here following the protocol described in McCune et al. 2019 » - “To validate that our methods are producing behavioral responses due to an inherent behavioral type”: consider replacing by “to test whether our methods are producing behavioral responses due to an inherent behavioral type”? (you do not have the answer already?) - consider adding the bold part in the following sentence: “whether performance on each task is correlated with performance on other tasks”? (or indicate to what it would be correlated here) - “on the two exploration tasks”: I am not sure readers will understand what the two tasks are here, so it may be better to mention them in full here by adding “(response to novel environment and to novel object)” – if I am right - Overall, the current version of the introductory section is very methodological oriented, but I think the writing of a standard manuscript following the analyses of resulting data will separate the objectives from methods in a more classical way (adding more info about previous literature to identify the biological questions to be explored). For now, I find this general presentation highly helpful and I am fully satisfied with it. - consider changing the bold parts in the following sentence: “we will attach a radio tag to each grackle and release them back” - “Furthermore, if space use behavior correlates with measures of exploration, then space use data could be used to inform conservation management strategies”: indeed, but this is not an objective of the present study since the study species is invasive! Probably something to highlight in the future discussion sections of the publications to follow. - I’m also fine regarding the “make more touches”; I did not have time to read the pre-registration describing the exploration tests in detail, but in any case, you will describe (even briefly) the tests in the manuscripts to follow, so the readers will not be disturbed by this point.

Preprint DOI: <http://corinalogan.com/Preregistrations/gspaceuse.html>

Author's reply:

Dear Dr.'s Blandine Doligez, Joe Nocera, Marion Nicolaus, and Laure Cauchard, Thank you for the thorough and thoughtful comments. We are grateful for the additional comments and the opportunity to revise and resubmit. We revised our preregistration and associated files at <http://corinalogan.com/Preregistrations/gspaceuse.html>, and we responded to your comments below. Note that the version-tracked version of this preregistration is in markdown at GitHub: <https://github.com/corinalogan/grackles/blob/master/Files/Preregistrations/gspaceuse.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 has been further improved due to additional feedback! All our best, Kelsey, Cody, Melissa, Luisa, and Corina

Does space use behavior relate to exploration in a species that is rapidly expanding its geographic range?

Kelsey B. McCune, Cody Ross, Melissa Folsom, Luisa Bergeron, Corina Logan

Recommender: Blandine Doligez

Comment 1: Dear authors, Thank you for your very detailed answers to our questions and comments in the last round, and in particular for adding a clear introductory section presenting the context of the study, the objectives, the general methods and potential implications. This section is currently a sort of a mix between introduction, methods and discussion as would be in a standard paper, and I think it will need to be reorganized in the manuscripts resulting from the study, but for now I am fully satisfied with this section that perfectly addresses my previous demand for a more dedicated section on presenting the study. In particular, I find the link between the individual processes and the population-level expansion question and the rationale for grouping the two main questions of interest here now much clearer; both aspects are now much better integrated (including in the title).

Response 1: We are very glad you are pleased with the revisions and that the introduction has clarified the links between our hypotheses.

Comment 2: I am therefore happy to recommend the pre-registration for PCI Ecology, and of course wish you good luck for the continuation of the project. I list below a few more details (and a few comments) that you could consider to still improving the text before publication.

Response 2: Thank you for your thorough and thoughtful comments. We incorporate and address them below.

Comment 3: Abstract : “Range expansion could be facilitated by individuals on the range edge that consistently differ in behavior compared to individuals in other parts of the range”: consider replacing by: “by consistent behavioural differences between individuals on the range edge and those in other parts of the range”?

Response 3: Your suggestion is a nice refinement of this sentence and we made this change.

Comment 4: “We will compare performance on an exploration task in captivity to subsequent space use behavior in the wild”: consider replacing by “we will test whether performance on an exploration task in captivity relates to subsequent space use behavior in the wild”?

Response 4: Thank you for this suggestion, we made this change.

Comment 5: add identify in “e.g. identify which individuals are likely to remain...”

Response 5: Thank you for this suggestion, we made this change.

Comment 6: Introduction: “Duckworth and Badyaev (2007) found that the more aggressive male western bluebirds dispersed the furthest”: strictly speaking, I do not think that these authors explored dispersal distance, but they found that new individuals in a population (defined as dispersers) were more aggressive. Consider rewording here accordingly?

Response 6: Thank you for pointing this out. We updated this sentence to say: “Duckworth and Badyaev (2007) found more aggressive behavior in western bluebird males on the range edge, suggesting that range expansion was facilitated by aggressive males dispersing further and displacing less aggressive mountain bluebirds.”

Comment 7: “thus facilitating the range expansion and displacing the less aggressive mountain bluebirds”: not sure that this is easily understandable for readers not familiar with this earlier paper, consider replacing by “thus facilitating the displacement of competing but less aggressive mountain bluebirds and favoring range expansion” or something like this?

Response 7: Please see Response 6.

Comment 8: citation for the definition of dispersal: instead of Cote et al. 2010, it would be more appropriate to cite Greenwood 1980 or 1982

Response 8: Good suggestion! We made this change and updated the definition of dispersal to that from Greenwood 1982: “the permanent movement an individual makes from its birth site to the place where it reproduces”

Comment 9: “novel foods, and food sources”: what do you mean here by distinguishing both?

Response 9: We mean here that there are novel types of foods, but also novel locations where food can be found. We updated this sentence to say: ...”novel foods, and novel food locations”...

Comment 10: consider adding the bold parts in the following sentence: “Traditional studies of animal space use required spatial and temporal independence of data points for statistical analysis (Swihart and Slade 1985). Yet, movement behavior is influenced by internal state, as well as the availability of habitat and resources, which can be distributed non-randomly across the landscape (Nathan et al. 2008), and movement data points are therefore and by construction unlikely to meet such spatio-temporal independence criteria.” (otherwise, which link do you make between these two sentences?)

Response 10: Good point, we incorporated your feedback into the changes we made for Response 11.

Comment 11: the 3rd paragraph is entirely methodological and comes a bit early in the manuscript, but this will certainly be re-adjusted in the resulting publication after the study is completed.

Response 11: Thank you for your feedback. We are aiming to follow a Registered Report format for this preregistration, which means that the introduction would not be editable after we conduct the study (to prevent posthoc biases from influencing our original ideas for this piece of research). However, we only decided that we needed to include the intro at the pre-study stage after this preregistration was peer reviewed, therefore we realize that the reviewers might have some changes to the introduction when we submit it at the post-study stage. As such, we would prefer not to change the introduction later on and so we address your comment at this time. We can see your point that it looks like this paragraph is methodological, but that is our fault for not bringing the main point of the paragraph to light in a more obvious way. This paragraph explains how we are achieving a research goal that is missing from previous literature, so we think it should stay in the introduction and we have revised it as follows:

Introduction paragraph 3: “Space use behavior is influenced by internal states like exploratory tendency and hunger, as well as the non-random distribution of available habitat and resources [[@nathan2008movement](#)]. Space use can also consistently differ among individuals [[@hertel2020guide](#)], which indicates that each individual has distinct preferences for how, when, and where to move within its home range. Traditional analyses of animal space use required spatial and temporal independence of data points for statistical analysis [[@swihart1985testing](#)], yet movement data are unlikely to meet these criteria. Instead, spatial and temporal autocorrelation, where individuals are repeatedly found in the same locations across time, is an intrinsic component of space use behavior and eliminating it can reduce biological relevance and obscure relationships with behavioral types [[@dray2010exploratory](#)]. Therefore, the autocorrelated nature of movement paths could be important to illuminate the relationship between individual differences in exploratory tendency and daily space use.”

Comment 12: 4th paragraph: I personally prefer to remain general as long as possible in the introduction and detail the study species specificities only in the methods, while keeping only general aims and objectives in the introduction. But again, you will see later on whether you wish to adjust the text accordingly in the resulting manuscripts.

Response 12: We would like to keep the species background in the introduction because we have heard from reviewers and recommenders of other preregistrations that they need this information sooner rather than later. Also, we are planning to format the post-study write up as Introduction, Results, Discussion, Methods so readers wouldn’t get this information until the very end.

Comment 13: internal state (singular)?

Response 13: Good catch, we updated this to clarify that there are multiple components of internal state: ..."internal states like exploratory tendency and hunger..."

Comment 14: "with these ecological and social factors which may vary": add a coma after factors

Response 14: Again, good catch! We removed this sentence while revising the Introduction.

Comment 15: first sentence of 5th paragraph: maybe make a transition here to start with (To better understand...), and I think it could be good to separate (i) the general objectives (testing the relation between exploratory tendency and space use behaviour) and (ii) the contexts for measuring these two behaviours (in captivity for exploration, in the wild for space use). This could simply be done by a slight change such as "We aim to understand whether measures of exploration, measured in captivity, are associated with space use behavior, measured in the wild, in grackles from three populations..." but importantly would place the focus back to the general objective.

Response 15: Thank you for the suggestions. We've updated the first sentence to include a transition phrase and your suggested rewording: "In this investigation, we aim to understand whether exploratory tendency, measured in captivity, is associated with space use behavior, measured in the wild, in grackles from three populations ..."

Comment 16: consider adding the bold part in the following sentence: "measured here following the protocol described in McCune et al. 2019 »

Response 16: Thank you for this suggestion, we made this change.

Comment 17: "To validate that our methods are producing behavioral responses due to an inherent behavioral type": consider replacing by "to test whether our methods are producing behavioral responses due to an inherent behavioral type"? (you do not have the answer already?)

Response 17: We are currently in the process of coding the videos of the exploration assays, so we do not yet know whether the methods elicit responses governed by an inherent behavioral type. We removed this sentence to make the Introduction less methodological, and it is in essence repeated in the section Methods > Summary of methods for measuring exploration.

Comment 18: consider adding the bold part in the following sentence: "whether performance on each task is correlated with performance on other tasks"? (or indicate to what it would be correlated here)

Response 18: We apologize for the confusion! We removed this sentence to make the Introduction less methodological, and it is in essence repeated in the section Methods > Summary of methods for measuring exploration.

Comment 19: "on the two exploration tasks": I am not sure readers will understand what the two tasks are here, so it may be better to mention them in full here by adding "(response to novel environment and to novel object)" – if I am right

Response 19: Please see Response 18.

Comment 20: Overall, the current version of the introductory section is very methodological oriented, but I think the writing of a standard manuscript following the analyses of resulting data will separate the objectives from methods in a more classical way (adding more info about previous literature to identify the biological questions to be explored). For now, I find this general presentation highly helpful and I am fully satisfied with it.

Response 20: As we mentioned in Response 11, we are aiming for a Registered Report type of process with this preregistration, and one of the purposes of this type of process is to prevent authors from revising their thinking about the research after the results have been seen. We addressed your comment now to reduce the amount of post-study editing to the introduction. We have removed much of the specific methodological detail from the Introduction that is repeated in the Methods section. Furthermore, we have added additional

background information and citations to make the relevance of the biological questions we address more clear.

Comment 21: consider changing the bold parts in the following sentence: “we will attach a radio tag to each grackle and release them back”

Response 21: We removed this sentence to make the Introduction less methodological, and it is in essence repeated in the section Methods > Planned sample.

Comment 22: “Furthermore, if space use behavior correlates with measures of exploration, then space use data could be used to inform conservation management strategies”: indeed, but this is not an objective of the present study since the study species is invasive! Probably something to highlight in the future discussion sections of the publications to follow.

Response 22: Good point! Definitely an interesting idea to incorporate in the future discussion section.

Comment 23: I’m also fine regarding the “make more touches”; I did not have time to read the pre-registration describing the exploration tests in detail, but in any case, you will describe (even briefly) the tests in the manuscripts to follow, so the readers will not be disturbed by this point.

Response 23: After reviewing more of the exploration videos we decided to remove “number of touches” to the novel object and novel environment as part of our exploration independent variable. There was a lot of skew in this response where a few grackles touched the items many times, but most did not touch them at all. We describe the exploration tests in the section Methods > Summary of methods for measuring exploration.

Revision round #2

2020-07-01

Does great-tailed grackle space use behavior reflect individual differences in exploration? Preregistration by Dr. Kelsey B. McCune, Dr. Cody Ross, Melissa Folsom, Luisa Bergeron, Dr. Corina Logan Review round 2

First of all, my deepest apologies for the long delay in processing the revision of your pre-registration. I believe that these past months have been difficult for all of us and the timing was particularly bad on my side...

Thank you for a thorough revision providing many details and adjustments to make the context and methods of the study clearer and take caution on the inferences that can be made from the results. The two reviewers (out of the three original ones) that could read your revised text and answers to their comments were happy with your changes, and my own reading also confirms that you have been able to satisfactorily take into account the comments of the last reviewer. We all agree that this work currently in progress will bring much information to relate individual behavioural traits to population-level processes, and as such, constitutes a highly valuable contribution to our understanding of movement (and expansion) processes.

When reading the revised version, two additional main comments / questions came to my mind, and I think it may be good to consider them before I recommend the preregistration.

First, the format of the preregistration still makes me feel a bit uncomfortable; I acknowledge that this is not a standard manuscript, yet the absence of a dedicated introduction clearly setting the context of the study makes it difficult to really understand some of the choices made in the methods. Currently, this context appears in part in the “abstract” (a longer version that lies in between a standard abstract and an introduction) and in part in the methods themselves to justify the variables, models used etc. Would it be possible to write a clear introduction section in a more standard way, that would provide more details about previous studies, what they have done and what remains to explore, and the implications of the work? The

current abstract section does not provide enough details about the context and rationale of the study (in particular, the transition to the second main prediction is inexistent, see also below). I think the preregistration would gain in clarity by adding a clear introduction and this would anyway be used in the future manuscripts resulting from the work. I would therefore consider adding this section, if it falls in the scope of preregistrations (not sure what format is required?)

Second (and this is also linked to the previous comment), I still think that the current presentation of the study and analyses leaves a gap between the individual and population processes that it aims to link. The ultimate aim of the work here is to relate (i) individual exploratory behaviour (measured in captivity), (ii) individual space use behaviour (measured in the field) and (iii) population-level expansion processes (through the among-population comparison across the species range). Yet, the two main hypotheses appear to only partly address this aim because one part is missing in this triptic: we will have no information about the differences in exploratory behaviour between the study populations, which would close the circle here and help understand whether individual differences in exploratory behaviour can at least partly explain species range expansion through individual space use. Thus I would suggest to (i) either add the among-population comparison of individual exploratory behaviour as a third axis of this work, or (ii) link more closely the two currently independent axes. As I suspect that the among-comparison in exploratory behaviour is planned to be part of another piece of work (?), maybe the second option would be best. In this case, why not simply consider a single model including the study population among the main effects of the model exploring the link between space use and exploratory behaviour (conspecific density can be considered at a small scale only, which seems to me more relevant to explain individual space use behaviour)? I understand that the data is limited and this would add one more explanatory variable to the models, but on the other hand it would avoid implementing separate models and allow testing more directly for a link to population processes that is currently missing to my opinion. Globally, both when presenting the study and in the statistical analyses planned, I would say that more effort seems to be needed to complete the exploration of the links between the three main variables of interest here (this is also apparent in the title, which does not mention the population and range expansion processes at all). I still think that making a clearer link between both predictions is needed for the coherence of the whole project. This would easily be done in a “real” introduction section here. Again, while this does not decrease the merits of the study, I believe that this point is likely to be raised by reviewers who will later on assess the manuscript out of the study. Thus maybe it could be good to better integrate the currently two axes of the work already here.

I also detail below a number of additional comments and questions (sorry there are no line numbers so it is not always easy to spot the location in the text), and attach a version of the text in which I have made suggestions and comments directly in the text.

- Abstract: “which could be subject to selection”: are you planning to investigate the genetic basis of exploration behaviour later on? Maybe a word on it as a perspective would be good...
- Prediction 1 alternative 1: it does not seem straightforward to me to link the use of a smaller area to higher efficiency; showing this may require an additional measure of this efficiency (e.g. foraging efficiency?).
- Prediction 1 alternative 2 and 3: but again, I think that the correlation between the different measures of exploration should be investigated first (before being related to space use). The authors mention it but it appears later on only, and it is not clear how this will be done overall (only correlations? what kind of models will be used? etc.)
- Table 1: please explain the number of years and generation presented for the first site
- I am wondering why the testing of 57 birds is anticipated rather than e.g. 60? Maybe there is no need to raise questions about an approximate number, and 60 (20 per site x 3 sites, half of each sex, thus 10 birds of each sex per site) reads more naturally than 57? I’d suggest replacing by 60, this remains the expected approximate sample size.
- “we are able to understand what this species is capable of, rather than testing juveniles who might still be developing their cognitive skills”: given that, as also noted in the text, adults may converge to

a common phenotype, what the species is capable of might however be expressed during the juvenile stage. Thus this justification is a bit strange to me?

- “so they fall off after one to four months”: this means that the comparison between space use behaviour during the breeding and non-breeding seasons is made across-individuals and not within-individuals: I think that this should be made clear in the text.
- “an experimenter tracks each tagged grackle for approximately 1.5 hours on a given day”: this is not totally clear as it gives the feeling that all birds are tracked every day, which appears not to be the case in the next sentence. This may need to be reformulated.
- “we aim to track all grackles equally during morning and afternoon time periods”: replace by “we aim to balance tracking data equally during morning and afternoon time periods for all grackles” (I if understand well)?
- “To account for alternative variables that may relate to space use behavior in wild grackles, we will also include covariates in our models that measure energetic condition (described in Berens et al. 2019), and habitat characteristics such as human food sources and available breeding habitat (described in Logan et al. 2019).”: this mention is fine overall, but more explanation (even brief) about why including these variables may be needed here (just as done for about conspecific density).
- “Each point will be visited once during the non-breeding season (Sep-Mar)”: a single count does not appear sufficient to provide a reliable estimate of density; the use of classical CMR methods requiring at least three counts may be needed. Or the reason why only one count will be performed needs to be explained here, along with the way to account for potential biases (e.g. if grackles show behavioural differences that affect detection probability between populations).
- “We catch grackles with a variety of methods”: at least describe all these methods used here (even briefly, with just their name)? or include a reference to another preregistration that describes them?
- “we attach radio tags to birds that do not participate in aviary tests”: explain here that this non-participation is due to the bird behaviour and not to other reasons (e.g. technical difficulties, choice of the experimenter or other).
- “times 1 and 2”: explain what these time periods are.
- “If there is a significant effect of season, we will run models separately for each dependent variable and each season”: why not simply including a season effect in the model and keep all data together? Unless behaviours are very different between both periods, this would be more powerful and also allow testing formal differences between seasons (through testing interactions between season and other variables).
- The sections “Methods” and “Analysis plan” show quite some repetitions, in particular in the descriptions of parameters / variables considered. Here again, the format used for this preregistration that differs from a standard manuscript may not appear optimal?
- “We will then model the relationship between bird-specific data on performance in the exploration tasks (and other covariates), and bird-specific movement parameters (e.g. step-size, turning angle, autocorrelation in space use).”: this is very brief and I think not sufficient to assess what statistical models will be used. Please provide details here.
- In particular: “The number of predictor variables was restricted to only the fixed effects because this test was not designed for mixed models.” but unless I missed it, the fixed vs. random effects are not described earlier?
- Check out the double parentheses issue with references.

Regarding your answers to the reviewers’ comments:

- Response 1: it may not be related to dispersal (but see comment below) but still, why do you not define your links as behavioural syndromes?
- Response 3: authors mention “...at both the individual and population level we have incorporated additional measures for data collection and analyses” but only one measure of density (group size, thus local density) seems to be considered later on, so this needs clarification (what variable refers to each of the two scales mentioned here?)

- Response 6: make clear that several females can breed on the territory defended by one (or more?) males, thus there is polygyny here (I found that this was not totally clear here).
- “we would have a biased sample”: I don’t understand this comment, especially as the proportion of non-participating birds caught with each of the two methods is compared later on to the proportion caught overall with each method, thus it is indeed possible to check for such biases (in participating to the tests and then for those participating, in the measures of exploration).
- By successive home ranges, I did not mean here between the breeding and non-breeding seasons, but during the same period, i. e. wandering birds that prospect from one place to another (or possibly use different home ranges successively over short periods of time). But then this does not seem to happen in this species, right? All adults (at least those caught) are in fact established over given determined territories? I think it may be a good idea to mention this clearly, as this is not true for all species. And this raises another thought: what if the processes of interest here, i. e. exploration, space use and ultimately colonization of new places, are in fact mostly occurring in juveniles during natal dispersal, while variation in these behaviours disappears in settled adults? An absence of differences between individuals / populations may be due to the age class considered here not being the most relevant here. I am not sure that this needs to be discussed in this pre-registration at this stage, but it might be something to keep in mind when results come in.
- Paragraph on power analyses: I’d suggest some rewriting, e.g. “To assess the effects that we will be able to detect given the expected sample size, we used GPower (v.3.1, @faul2007g, @faul2009statistical) to conduct power analyses based on confidence intervals. GPower uses pre-set drop down menus and we chose the options that were as close to our analysis methods as possible (listed in each analysis below). [...] These power analyses are not fully aligned with our study design, and the expected effect sizes are difficult to estimate due to the lack of prior data on this species; yet we are unaware of current better options.”
- “our interest in decreasing noise by attempting to measure it, which increases the number of explanatory variables”: I do not understand this section, and thus suggest to either delete or explain it in more detail? How do you measure noise by increasing explanatory variables? Please rephrase here.
- Response 25: I am not sure to understand the link between fitness / adaptation and sex biases in dispersal. I concur with the reviewer here that the evolutionary aspect is not part of the present project and thus that it would be better not to mention it here to start with (but could be done in the discussion section) and possibly leave it to other parts of the study (other pre-registrations, as mentioned here).
- “Regarding dispersal syndromes, to us dispersal would refer to grackles moving out of the natal area when they are young and/or as adults searching for new territories. However, this type of longer-distance movement (and tracking of young birds) is beyond the scope of this investigation. Therefore, we are not investigating the effect of consistent behavioral differences in population dynamics.” While I agree with this answer at a detailed scale, the link is nevertheless made with evolutionary population dynamics through the study of three different populations at different stages of range expansion. Thus I still agree with the reviewer that dispersal / colonization syndromes are at play here, even if the variables investigated here are not directly dispersal – it seems implicit in the study design (otherwise, why compare these populations?)
- “but it is still unknown whether individual differences in exploration relate to daily movement patterns”: I’d replace this by “but it is still unknown whether such relationships rely on links between individual differences in exploration and daily movement patterns”.
- Response 30: even if there is no connectivity between the three study populations (which indeed does not seem plausible given the between-population distances!) I believe that the reviewer was thinking more in terms of connectivity between adjacent populations: if there are a network of highly connected populations, differences may disappear quickly. Maybe a word could be added here about whether many connected populations can be found around the study populations chosen here, or in other words whether the grackle populations form a continuous network of connected

populations (even if dispersal occurs at a limited spatial scale). Also, was the discussion about turnover speed somehow evoked in the text?

- Be careful not to use interchangeably neophobia and boldness, both traits have different definitions, as noted in the text: boldness includes a notion of risk to the individual while neophobia does not. They are usually considered two different personality traits for this reason. Boldness involves that individuals identify a specific risk before displaying a reaction, e.g. when a dummy predator is present.
- “Many studies that measure animal personality using novel objects have similarly used the same objects in two (or more) repeated exposures and found that responses are repeatable (e.g. @mccune2018personality). If there is habituation to the object because it has become familiar after Time 1, this will likely affect all individuals similarly and we will still be able to detect overall repeatability in behavior”. While I agree with the first part of the statement (the use of the same object repeatedly on the same individuals in different tests, in most cases to make sure indeed the same level of stimulation / motivation is reached, as mentioned here), I am not sure that I agree with the end part: habituation to an object may differ between individuals – I would even say that it can be expected to differ between individuals! Yet, no ideal design for such tests exists (using the same object repeatedly vs. changing objects both have their drawbacks), thus I have no problem with using the same object in several tests, but I think it is necessary to acknowledge the limitation that this repeated use imposes.
- “Based on these findings, it is unlikely that the aviary grackles that are released back to the wild change social groups or home ranges.” Even if this sounds highly plausible, it remains necessary to formally show it by tracking individuals not held in captivity as mentioned just after.
- “It is possible that grackles that participate in aviary tests are more bold and exploratory than conspecifics that were never in the aviaries.” Why would it be so? Do you suggest that spending time in the aviaries may change the behavioural responses of the birds post-release? Or do you suggest that the birds initially placed in aviaries are not representative of the whole population, and if yes, why? Please can you explain?
- “so that our question solely refers to adult behavior”: fine but large differences are usually reported (especially with regards to behaviour) between one-year-old and older adults, as mentioned by the reviewer. Because it is not possible to distinguish these two age categories here, as detailed by the authors, it could be good to mention this point clearly (to avoid further questions by future referees).

Preprint DOI: <http://corinalogan.com/Preregistrations/gspaceuse.html>

Reviewed by [Joe Nocera](#), 2020-05-05 19:46

I commend the authors on a very thorough revision; responses to each and every reviewer comment were well thought out. In deference to the other reviewers, I will limit my comments here to only those that I raised in Round #1.

Regarding sample sizes and a priori power analyses: Your response here is perfect. GPower is exactly the program I use for this. You are correct that it is often difficult to guess an estimated effect size. Generally, we are limited to what we know from the literature or from studies on other seemingly-related species. It is not a perfect art, but it is instructive. As such, we now have greater (quantifiable) assurance that your sample size of ~57 will be adequate.

Observer effects on radio-tracking: Ok, I'll buy that. Knowing these birds are exposed to humans regularly makes me feel better about it. Good to now have clarified that in the document.

MCPs and AKDE: I am very happy to see that you agree AKDE is a preferable analytical method here. I hope it works well for you, and you are welcome for the suggestion. ctm and sf are the two packages I would have suggested.

Habitat: Ok, I was unaware that habitat data were part of a previously submitted document. Good to now mention that within the text of this document.

Overall, I am very happy with the revisions the authors made in regards to my comments in Round #1. I think this new version is great. Best of luck!

Joe N

Reviewed by [Laure Cauchard](#), 2020-05-05 22:37

Round 2

Response 40, 1: ok! Response 40, 2: a way to be sure that neophobia does not interfere with your exploration test would be to conduct the test without food (if the birds are used to come into the test room for the food, they will continue to do it even if you remove it for 1 time) for a small number of birds and compare the results with the exploration test with food. If your results are correlated it should be ok. But I am not sure about a neophobia test with an object related to predators? The strength of the neophobia's response can vary with the previous experience of the bird with a real predator and blurs the response to novelty you are measuring. I know that many studies use the same object to measure repeatability of neophobia but I am just not sure if they measure the repeatability of neophobia and not the repeatability of habituation/exploration as it is not a novel object anymore... But it is only my opinion, and you have excellent refs to refer to so it is ok with the same object. And I totally understand if your tests are already done in one of the populations, you cannot change it for the others...

Response 41: I did not see the other birds were color marked and I was wondering how you would know that it was the same bird if they were not tagged at all... Sorry!

Response 42: ok!

Response 43: ok!

Response 44: I totally understand the problem here. Yet, this species is quite long living for a bird and age/experience might then play an important role. If you would be able to find a way to evaluate age, it would be very interesting. Maybe you can use a first-time-seen age for those birds you see several years even if you don't know their age at the first capture? Or maybe through telomere loss if it is possible with your species?

Good luck for your project, it is very interesting!

Author's reply:

Dear Dr.'s Blandine Doligez, Joe Nocera, Marion Nicolaus, and Laure Cauchard, We greatly appreciate the time you have taken to give us such useful feedback and to follow up on our revisions from round one. We are very thankful for your willingness to participate in the peer review of preregistrations, and we are happy you found that our revisions improved this preregistration. We are grateful for the additional comments and the opportunity to revise and resubmit. We revised our preregistration and associated files at <http://corinalogan.com/Preregistrations/gspaceuse.html>, and we responded to your comments below. Note that the version-tracked version of this preregistration is in markdown at GitHub: <https://github.com/corinalogan/grackles/blob/master/Files/Preregistrations/gspaceuse.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 has been further improved due to additional feedback! All our best, Kelsey, Cody, Melissa, Luisa, and Corina

Does space use behavior relate to exploration in a species that is rapidly expanding its geographic range?

Kelsey B. McCune, Cody Ross, Melissa Folsom, Luisa Bergeron, Corina Logan

Recommender: Blandine Doligez

Comment 1: First of all, my deepest apologies for the long delay in processing the revision of your pre-registration. I believe that these past months have been difficult for all of us and the timing was particularly bad on my side...

Response 1: Thank you so much for committing to giving us thoughtful and detailed comments. We understand the time and focus it takes to review a manuscript for scientific integrity, especially during this pandemic.

Comment 2: Thank you for a thorough revision providing many details and adjustments to make the context and methods of the study clearer and take caution on the inferences that can be made from the results. The two reviewers (out of the three original ones) that could read your revised text and answers to their comments were happy with your changes, and my own reading also confirms that you have been able to satisfactorily take into account the comments of the last reviewer. We all agree that this work currently in progress will bring much information to relate individual behavioural traits to population-level processes, and as such, constitutes a highly valuable contribution to our understanding of movement (and expansion) processes.

Response 2: We are really glad that you think this work is valuable, and that you are pleased with our revisions.

Comment 3: When reading the revised version, two additional main comments / questions came to my mind, and I think it may be good to consider them before I recommend the preregistration. First, the format of the preregistration still makes me feel a bit uncomfortable; I acknowledge that this is not a standard manuscript, yet the absence of a dedicated introduction clearly setting the context of the study makes it difficult to really understand some of the choices made in the methods. Currently, this context appears in part in the "abstract" (a longer version that lies in between a standard abstract and an introduction) and in part in the methods themselves to justify the variables, models used etc. Would it be possible to write a clear introduction section in a more standard way, that would provide more details about previous studies, what they have done and what remains to explore, and the implications of the work? The current abstract section does not provide enough details about the context and rationale of the study (in particular, the transition to the second main prediction is inexistent, see also below). I think the preregistration would gain in clarity by adding a clear introduction and this would anyway be used in the future manuscripts resulting from the work. I would therefore consider adding this section, if it falls in the scope of preregistrations (not sure what format is required?)

Response 3: We understand the format is a bit strange. We have created an introduction section, and revised the abstract, hypotheses and methods to remove some of the introductory-type material. We hope this improves clarity and understanding of the impact of this study.

Comment 4: Second (and this is also linked to the previous comment), I still think that the current presentation of the study and analyses leaves a gap between the individual and population processes that it aims to link. The ultimate aim of the work here is to relate (i) individual exploratory behaviour (measured in captivity), (ii) individual space use behaviour (measured in the field) and (iii) population-level expansion processes (through the among-population comparison across the species range). Yet, the two main hypotheses appear to only partly address this aim because one part is missing in this tryptic: we will have no information about the differences in exploratory behaviour between the study populations, which would close the circle here and help understand whether individual differences in exploratory behaviour can at least partly explain species range expansion through individual space use. Thus I would suggest to (i) either add the among-population comparison of individual exploratory behaviour as a third axis of this work, or (ii) link more closely the two currently independent axes. As I suspect that the among-comparison

in exploratory behaviour is planned to be part of another piece of work (?), maybe the second option would be best. In this case, why not simply consider a single model including the study population among the main effects of the model exploring the link between space use and exploratory behaviour (conspecific density can be considered at a small scale only, which seems to me more relevant to explain individual space use behaviour)? I understand that the data is limited and this would add one more explanatory variable to the models, but on the other hand it would avoid implementing separate models and allow testing more directly for a link to population processes that is currently missing to my opinion. Globally, both when presenting the study and in the statistical analyses planned, I would say that more effort seems to be needed to complete the exploration of the links between the three main variables of interest here (this is also apparent in the title, which does not mention the population and range expansion processes at all). I still think that making a clearer link between both predictions is needed for the coherence of the whole project. This would easily be done in a “real” introduction section here. Again, while this does not decrease the merits of the study, I believe that this point is likely to be raised by reviewers who will later on assess the manuscript out of the study. Thus maybe it could be good to better integrate the currently two axes of the work already here.

Response 4: We hope we have provided more clear links and motivations between the goals of this preregistration in the new Introduction section. You are right that this preregistration does not address cross-population differences in exploration because we had already planned to include that in a separate preregistration focusing on cross population differences that is in prep (<http://corinalogan.com/Preregistrations/gxpopbehaviorhabitat.html>). It is difficult a priori to split our large long-term research program into smaller pieces and to decide where the various pieces belong. As stated in the section A. State of the Data, this space use preregistration was developed after the larger overarching research program (including a cross-population study of exploration) was already planned. So the analysis of exploratory tendency across populations will be in the separate cross-population preregistration, and, at least for this phase of the research (preregistration and pre-study peer review), we’d like to keep the focus of the space use preregistration on the movement behavior.

Thank you for pointing out that our title does not adequately capture our whole study. We updated it: Does space use behavior relate to exploration in a species that is rapidly expanding its geographic range?

Additionally, our analysis for H1 will tell us whether exploration is correlated with space use and, if so, then we will be able to infer that results from the analyses of movement behavior across populations (H2) likely also apply to exploration. If exploration and space use are not related (based on results from H1), then we will understand how space use varies across populations (H2) and we will also understand how exploration varies across populations based on results from the separate cross-population preregistration.

Comment 5: I also detail below a number of additional comments and questions (sorry there are no line numbers so it is not always easy to spot the location in the text), and attach a version of the text in which I have made suggestions and comments directly in the text.

Response 5: Thank you for these edits! We have incorporated all of your wording changes throughout the preregistration.

There are 2 questions you raised in the comments of the PDF that we address here:

Comment B1: You wrote “Is this relevant for and abstract? Maybe delete this part here.” This piece is now deleted from the Abstract as we have updated the Abstract to reflect the new Introduction section, included per your Comment 3. Please see these new sections.

Comment B5: You wrote “more touches to the novel environment? This may require reformulation.” The novel environment that we use is a small pop-up tent made for cats that we put inside the familiar environment of the bird’s aviary. Therefore, it does occur that the grackles touch different parts of the tent. There is also variation in how many touches a grackle makes, or whether grackles touch the tent at all.

Comment 6: Abstract: “which could be subject to selection”: are you planning to investigate the genetic basis of exploration behaviour later on? Maybe a word on it as a perspective would be good...

Response 6: We do not currently have plans to investigate the genetic basis of exploration in grackles. Additionally, we are investigating cross-population variation in exploration in a separate preregistration, so we have deleted this statement from this preregistration because it is not really relevant.

Comment 7: Prediction 1 alternative 1: it does not seem straightforward to me to link the use of a smaller area to higher efficiency; showing this may require an additional measure of this efficiency (e.g. foraging efficiency?).

Response 7: We apologize for the confusion, we see that “efficiency” is perhaps the wrong word here. Currently, we do not have a good measure for foraging efficiency so we would not be able to test this. We have updated this prediction to emphasize that more exploratory grackles may spend more time investigating smaller areas. In general, we include speculation for why our results might support an alternative prediction to stimulate future research on that topic. But it is not necessarily something we are able to test in this current preregistration. Prediction 1 alternative 1 now reads (changes in boldface text):

“The more exploratory grackles will be found in a smaller expanse (smaller home range size), use more predictable movement patterns (high autocorrelation of step lengths and turning angles), and consistently occupy the same spatial locations. This would suggest that the more exploratory individuals **may dedicate more time to investigating a smaller area within their home range rather than moving into new areas for resources such as food or mating opportunities.**”

Comment 8: Prediction 1 alternative 2 and 3: but again, I think that the correlation between the different measures of exploration should be investigated first (before being related to space use). The authors mention it but it appears later on only, and it is not clear how this will be done overall (only correlations? what kind of models will be used? etc.)

Response 8: Yes, in the Exploration preregistration that has already passed peer-review we do investigate the correlation between the measures and we discuss the models that we will use. Since we already have the information about our methods to measure and analyze performance on exploration tasks in the Exploration preregistration, in this Space Use preregistration we want to keep the focus on the space use behavior, measures, and analyses. We included a summary of the methods from the Exploration preregistration in this current preregistration in Methods > Summary of methods for measuring exploration:

“We adapted commonly used methods to test exploratory tendency of the grackles that are temporarily held in aviaries in response to a novel environment and a novel object. Exploration assays occur twice for each bird: once near the beginning of their aviary time (“time 1”) and once again approximately 6 weeks later (“time 2”). Habituation may occur between time 1 and time 2, decreasing the novelty of the experimental setup. However, it is common practice to use the same setup across the repeated assays because it is very difficult to predict how threatening a novel object will be to a grackle. Therefore, if we accidentally introduce objects that are much more or much less threatening across the two time periods, this could obscure our ability to determine whether there are consistent individual differences with regard to these particular novel objects. We will analyze whether behavioral responses during assays are repeatable within individuals and whether exploration of a novel environment correlates with exploration of a novel object, indicating they are measures of the same inherent trait. If the two exploration measures are consistent within individuals and correlate with each other, we will choose as the exploration score the variable with the most data. If the two measures do not correlate, we will include both as independent variables.”

We have also clarified that we will do this before relating the measures to space use early on in the preregistration in the new Introduction:

“To validate that our methods are producing behavioral responses due to an inherent behavioral type, in [McCune et al. 2019](#) we first verify the repeatability of performance on each exploration task, then we determine whether performance on each task is correlated. If responses are repeatable and performance is

correlated, we will take as the exploration score the variable for which we have the most data. If performance on the two exploration tasks is not correlated, we will include both as independent variables representing potentially different aspects of the behavioral type.”

Comment 9: Table 1: please explain the number of years and generation presented for the first site

Response 9: Sorry about this oversight! We forgot to include this information in the revision, so thank you for catching this. We added to the table 1 legend:

“Table 1. Population characteristics for each of the three field sites. The number of generations at a site is based on a generation length of 5.6 years for this species (International (2018)) and on the first year in which this species was reported to breed at the location (Wehtje (2003) for Arizona, Steve Hampton’s pers. comm. reported in Pandolfino, Deuel, and Young (2009) for Woodland, California). The first confirmed nest sighting in Woodland, California was reported in the Yolo Audubon Society’s newsletter *The Burrowing Owl* (July 2004), which Steve Hampton shared with Logan. For Central America, there is no data on the first year in which they started breeding because this species originates in this region, therefore we used the age of the species: 800,000 years (Johnson and Cicero (2004)).”

Comment 10: I am wondering why the testing of 57 birds is anticipated rather than e.g. 60? Maybe there is no need to raise questions about an approximate number, and 60 (20 per site x 3 sites, half of each sex, thus 10 birds of each sex per site) reads more naturally than 57? I’d suggest replacing by 60, this remains the expected approximate sample size.

Response 10: Thank you for pointing this out. You are correct in that we estimate approximately 20 birds per site will be tested and we won’t know for sure what our sample sizes will be until we are done collecting the data, therefore anything other than a round number is unnecessary. We have updated our sample size to be 60 in Methods > Sample Size Rationale

We also updated our power analysis in Analysis Plan > Ability to detect actual effects > H1 & H2 from $n = 57$ to $n = 60$

Comment 11: “we are able to understand what this species is capable of, rather than testing juveniles who might still be developing their cognitive skills”: given that, as also noted in the text, adults may converge to a common phenotype, what the species is capable of might however be expressed during the juvenile stage. Thus this justification is a bit strange to me?

Response 11: We apologize for the confusion! Other studies documenting the behavioral expression of cognitive traits indicate that hatch year birds (juveniles) often do not have fully developed traits (i.e. object permanence, Zucca et al. 2007). Logistically, we did not have the time or ability to incorporate a longitudinal study to document what traits juveniles have, or when they develop them. By testing only adults, the progression of cognitive traits is relatively more complete, therefore we can assume that we have eliminated the potential confounding factor of stage of cognitive development.

To clarify, we have updated this statement in Methods > Planned Sample:

... “Cognitive and behavioral traits are often not fully developed in hatch year birds (i.e. Zucca et al. 2007). For our aviary cognitive test battery, we avoided the potentially confounding variable of stage of cognitive development by only taking known adult grackles into the aviaries. We identified grackles as adults using eye color, where hatch year birds have brown eyes, but second year and older birds have yellow eyes. While it is possible that cognitive traits continue to develop in second year and older birds, it is impossible to distinguish grackle age after the bird’s first year (Johnson and Peer 2001)”...

Comment 12: “so they fall off after one to four months”: this means that the comparison between space use behaviour during the breeding and non-breeding seasons is made across-individuals and not within-individuals: I think that this should be made clear in the text.

Response 12: Yes, thank you for pointing this out. Originally, the tag battery life indicated that we would be able to follow birds across seasons. However, in practice, the harnesses we used to attach radio tags to grackles degraded and fell off at variable intervals. We have clarified this in Methods > Planned Sample:

“We hoped to track the same individuals across the breeding and nonbreeding seasons. However, the leg loop harnesses often degraded and fell off after 1 - 4 months. Therefore, we have few data points on the same individuals in both seasons, and we will instead compare space use in different individuals (rather than within individuals) across seasons.”

Comment 13: “an experimenter tracks each tagged grackle for approximately 1.5 hours on a given day”: this is not totally clear as it gives the feeling that all birds are tracked every day, which appears not to be the case in the next sentence. This may need to be reformulated.

Response 13: We are sorry this was confusing and we have updated these statements in Methods > Planned Sample to read:

“After release, an experimenter will find and follow (each session is called a “track”) each tagged grackle at least four times per week to obtain as much data on space use as possible. On each of these tracks, the experimenter follows the focal individual for approximately 1.5 hours, recording a GPS point every one minute, regardless of whether the bird moved [[@cushman2005elephants](#)]...”

Comment 14: “we aim to track all grackles equally during morning and afternoon time periods”: replace by “we aim to balance tracking data equally during morning and afternoon time periods for all grackles” (I if understand well)?

Response 14: Thank you for the suggestion, we have made this change.

Comment 15: “To account for alternative variables that may relate to space use behavior in wild grackles, we will also include covariates in our models that measure energetic condition (described in [Berens et al. 2019](#)), and habitat characteristics such as human food sources and available breeding habitat (described in [Logan et al. 2019](#)).”: this mention is fine overall, but more explanation (even brief) about why including these variables may be needed here (just as done for about conspecific density).

Response 15: Good point. We have updated this paragraph to elaborate on why these variables are also important as follows in Methods:

“Exploratory tendency is an intrinsic factor that could be related to space use behaviors. However, there are also likely alternative variables that may relate to space use behavior in wild grackles that we must control for by including them as covariates in our models. First, we measure energetic condition (described in [Berens et al. 2019](#)) to account for differences in the physiological mobility that may limit an individual’s space use behaviors ([@nathan2008movement](#)). Secondly, we measure habitat characteristics such as human food sources and available breeding habitat (described in [Logan et al. 2019](#)) because these factors of the external environment will affect where grackles choose to move or spend time ([@nathan2008movement](#)).”

Comment 16: “Each point will be visited once during the non-breeding season (Sep-Mar)”: a single count does not appear sufficient to provide a reliable estimate of density; the use of classical CMR methods requiring at least three counts may be needed. Or the reason why only one count will be performed needs to be explained here, along with the way to account for potential biases (e.g. if grackles show behavioural differences that affect detection probability between populations).

Response 16: We apologize for the oversight of not detailing the point count analysis more thoroughly. We have now added text that clearly details how we intend to quantify density in each region. It states in Analysis Plan:

“We will quantify region-specific grackle density by fitting a hierarchical model that accounts for imperfect detection. Specifically, we will use the model developed by [@amundson2014hierarchical](#) which integrates data on time of detection and distance estimates to account for the probability a bird is available to be

detected (p_a), and the probability it is detected given it is available (p_d), respectively (@nichols2009inference). All parameters (density, p_a , and p_d) will be modeled as a function of region. Because we expect that vocalization rates will be greater for males than females, we will also model p_a as a function of sex. We will extract the estimate of expected point-level density for each region and use this estimate as the covariate in our movement models.”

For the purposes of our analysis, we are interested in an estimate of the expected density of a region. For this reason, we want spatial replication of samples because this will give us a better estimate of the average density across points in the region, rather than repeated sampling at individual locations (which would give us better point-level density estimates). Amundson et al. (2014) found that repeated sampling is not necessary to estimate imperfect detection because the model uses distance and time of detection information for that purpose. The survey effort we are proposing is on par with the single-visit sampling approaches used in other studies (e.g., Sillett et al. 2012).

Amundson, C. L., Royle, J. A., & Handel, C. M. (2014). A hierarchical model combining distance sampling and time removal to estimate detection probability during avian point counts. *The Auk: Ornithological Advances*, 131(4), 476-494.

Sillett, T. S., Chandler, R. B., Royle, J. A., Kéry, M., & Morrison, S. A. (2012). Hierarchical distance-sampling models to estimate population size and habitat-specific abundance of an island endemic. *Ecological Applications*, 22(7), 1997-2006.

Comment 17: “We catch grackles with a variety of methods”: at least describe all these methods used here (even briefly, with just their name)? or include a reference to another preregistration that describes them?

Response 17: Good catch, it makes sense to name the methods. We have added this as follows to Sample size rationale:

“We catch grackles with a variety of methods (mist nets, walk-in traps, and bow nets)”...

Comment 18: “we attach radio tags to birds that do not participate in aviary tests”: explain here that this non-participation is due to the bird behaviour and not to other reasons (e.g. technical difficulties, choice of the experimenter or other).

Response 18: Good point. We have updated this sentence as follows to Sample Size Rationale:

“Additionally, we attach radio tags to birds that are released early because of their lack of willingness to participate in aviary tests (currently 5 individuals) to determine whether space use behavior differs between participatory and non-participatory grackles.”

Comment 19: “times 1 and 2”: explain what these time periods are.

Response 19: We clarified that times 1 and 2 indicate each instance of the repeated exploration assays in Methods > Summary of methods for measuring exploration:

“We adapted commonly used methods to test exploratory tendency of the grackles that are temporarily held in aviaries in response to a novel environment and a novel object. Exploration assays occur twice for each bird: once near the beginning of their aviary time (“time 1”) and once again approximately 6 weeks later (“time 2”). ”...

Comment 20: “If there is a significant effect of season, we will run models separately for each dependent variable and each season”: why not simply including a season effect in the model and keep all data together? Unless behaviours are very different between both periods, this would be more powerful and also allow testing formal differences between seasons (through testing interactions between season and other variables).

Response 20: This is a good idea, thank you for the suggestion. We have updated Methods > Independent variables > P1 and P2 so that there is a “Season” variable. We removed the statements about season in the Analysis Plan and we also updated the analysis code for the P1 and P2 models to reflect this addition.

Comment 21: The sections “Methods” and “Analysis plan” show quite some repetitions, in particular in the descriptions of parameters / variables considered. Here again, the format used for this preregistration that differs from a standard manuscript may not appear optimal?

Response 21: Thanks for pointing this out. We have removed the components from the Analysis plan that were already stated in the Methods or in the description of the independent and dependent variables.

Comment 22: “We will then model the relationship between bird-specific data on performance in the exploration tasks (and other covariates), and bird-specific movement parameters (e.g. step-size, turning angle, autocorrelation in space use).”: this is very brief and I think not sufficient to assess what statistical models will be used. Please provide details here.

Response 22: We have added more detail to this point in the Analysis Plan as follows: “We will then model the relationship between **independent variables describing** bird-specific data on performance in the exploration tasks and other covariates (**as outlined above**), and bird-specific movement parameters (e.g. home range size, autocorrelation in step-size and turning angle, repeatability of spatial location preferences) **as our dependent variables. We will use linear models and we will ensure assumptions of normality are met by checking that the residuals from our fitted models are normally distributed.**”

Comment 23: In particular: “The number of predictor variables was restricted to only the fixed effects because this test was not designed for mixed models.” but unless I missed it, the fixed vs. random effects are not described earlier?

Response 23: Thank you for catching this! This is an error that carried over from a different preregistration. There are no random effects currently in these models, so we have removed this statement.

Comment 24: Check out the double parentheses issue with references.

Response 24: Thank you for pointing this out, we had not noticed this before. We have streamlined our in-text citations throughout.

Comment 25: Regarding your answers to the reviewers’ comments (in Rebuttal 1):

(R1) Response 1: it may not be related to dispersal (but see comment below) but still, why do you not define your links as behavioural syndromes?

Response 25: We cannot say *a priori* whether the performance of the grackles on our personality assays will correlate to form a behavioral syndrome. Furthermore, we do not know *a priori* whether performance will be repeatable, indicating that our assays are valid measures of an inherent trait. Therefore, we do not know if performance represents behavioral syndromes, distinct personality traits, or behavior influenced by a given temporary context (hunger, fear, boredom) rather than a personality trait.

Comment 26: (R1) Response 3: authors mention “...at both the individual and population level we have incorporated additional measures for data collection and analyses” but only one measure of density (group size, thus local density) seems to be considered later on, so this needs clarification (what variable refers to each of the two scales mentioned here?)

Response 26: The two measures are: 1. Group size at an individual level, measured during focal follows (i.e. the individual’s sociality) and 2. Conspecific density at the population level measured with point count surveys.

At the individual level we are measuring the preferred social group size of an individual and not local conspecific density. “Density” refers specifically to the expected point-level population density estimated

from our point count model. As noted in Response 16 above, we have now added additional details to the preregistration to explain how these estimates are generated.

We apologize that we forgot to add Density to our P2 analysis code. We have updated that now.

Comment 27: (R1) Response 6: make clear that several females can breed on the territory defended by one (or more?) males, thus there is polygyny here (I found that this was not totally clear here).

Response 27: We have moved this content into the new Introduction and revised it as follows:

...”During the breeding season, one or more males defend a territory and **multiple** females place their nests within the same territories to raise the young”...

Comment 28: (R1) “we would have a biased sample”: I don’t understand this comment, especially as the proportion of non-participating birds caught with each of the two methods is compared later on to the proportion caught overall with each method, thus it is indeed possible to check for such biases (in participating to the tests and then for those participating, in the measures of exploration).

Response 28: We meant here that we only have measures of performance on our exploration assays from individuals that successfully habituate to the aviaries and progress through the first experiment. Only after their first experiment do the aviary grackles receive the exploration test. If grackles don’t habituate or participate in the first experiment we must quickly release and replace them to maintain an adequate sample size for the entire aviary test battery. Theoretically, these birds do not participate because they are on the shy, non-exploratory end of the spectrum for these traits. However, we cannot know this for sure because we did not give them exploration assays. That is why we decided it was necessary to measure the space use behavior of non-participating grackles in addition to those that had participated in aviary tests - to quantify whether this bias exists and is reflected in movement behavior.

Because we do not have measures of exploration and boldness from all birds caught with the different trapping methods we cannot model the relationship between trapping method and performance on our exploration assay. All we can do is look at the number of grackles that had to be released from the aviaries for not participating in relation to trapping method. But this assumes participation in aviary tests is governed by boldness and exploration, which although likely, we did not explicitly test.

Comment 29: (R1) By successive home ranges, I did not mean here between the breeding and non-breeding seasons, but during the same period, i. e. wandering birds that prospect from one place to another (or possibly use different home ranges successively over short periods of time). But then this does not seem to happen in this species, right? All adults (at least those caught) are in fact established over given determined territories? I think it may be a good idea to mention this clearly, as this is not true for all species.

Response 29: It is possible that wandering grackles occur, or that territoriality exists on more of a spectrum among individuals. This is exactly what we hope to quantify as potentially reflecting the exploration trait. Most of the adults that we catch stay in a similar enough area that we can repeatedly find them, even without radio telemetry. We cannot say on a more empirical level whether they are using successive home ranges, or prospecting different habitats until we analyze these data. However, the way in which we will analyze the data will tell us whether individuals are always in the same place (high repeatability of spatial preferences), or if they move to new places daily or weekly.

We have elaborated on this in the new Introduction as follows:

... “Although we know that there are general territorial behaviors related to the breeding system of this species, it is unknown how space use behavior varies within individuals across time and across individuals.”...

Comment 30: And this raises another thought: what if the processes of interest here, i. e. exploration, space use and ultimately colonization of new places, are in fact mostly occurring in juveniles during natal dispersal, while variation in these behaviours disappears in settled adults? An absence of differences

between individuals / populations may be due to the age class considered here not being the most relevant here. I am not sure that this needs to be discussed in this pre-registration at this stage, but it might be something to keep in mind when results come in.

Response 30: We appreciate these thoughts and will be prepared to address this in the discussion in the resulting publication. We anticipate that we could find null results given that much of the literature on dispersal reflects the greater occurrence of this type of movement in juveniles. However, we are not logistically able to measure either long-distance dispersal, or juveniles. If we find no relationship between space use behaviors and study site location, this will still be a valuable contribution to our knowledge of movement ecology, and potentially a platform motivating further study of juvenile natal dispersal. We believe there is value in investigating daily space use behaviors of adult individuals from populations that span the geographic range. Research in other taxa (e.g. cane toads, crayfish) find variation in *adult* movement behaviors at different time points in the invasion process (i.e. pioneer individuals move more than later generations at a study site). Furthermore, ecological and social factors will be different for individuals in different parts of the range, and it will be informative to see how these covariates interact with space use behavior.

We have clarified these points in the new Introduction. We have also updated H2 > Prediction 2 alternative 2:

“We will find no difference across the geographic range in the space use behavior of the grackles sampled. This would suggest that, on average, all grackles may use the same amount of space, or that there is a similar distribution of individual differences in space use in each population. **Alternatively, it could indicate that we did not detect differences because we measured adults rather than juveniles. Grackles sampled in different populations may converge on similar space use behavior during development, or juvenile grackles may disperse further on the edge of the range. However, we are not able to detect these differences with our data, which is primarily from adults.**”

Comment 31: Paragraph on power analyses: I’d suggest some rewriting, e.g. “To assess the effects that we will be able to detect given the expected sample size, we used GPower (v.3.1, @faul2007g, @faul2009statistical) to conduct power analyses based on confidence intervals. GPower uses pre-set drop down menus and we chose the options that were as close to our analysis methods as possible (listed in each analysis below). [...] These power analyses are not fully aligned with our study design, and the expected effect sizes are difficult to estimate due to the lack of prior data on this species; yet we are unaware of current better options.”

Response 31: Thank you very much for your suggestion! We replaced the text with the text you wrote above.

Comment 32: “our interest in decreasing noise by attempting to measure it, which increases the number of explanatory variables”: I do not understand this section, and thus suggest to either delete or explain it in more detail? How do you measure noise by increasing explanatory variables? Please rephrase here.

Response 32: This part of the sentence was deleted per your re-writing in Comment 31, therefore we did not add an explanation for it to the revision. The idea was to explain that there may be many variables linked to a given response variable. These variables are generally considered “noise” unless we measure some of them, in which case they become independent variables and are therefore no longer noise. It’s not an important distinction to make though so the paragraph as you modified it is sufficient.

Comment 33: (R1) Response 25: I am not sure to understand the link between fitness / adaptation and sex biases in dispersal. I concur with the reviewer here that the evolutionary aspect is not part of the present project and thus that it would be better not to mention it here to start with (but could be done in the discussion section) and possibly leave it to other parts of the study (other pre-registrations, as mentioned here).

Response 33: We agree that we should keep this piece separate. Response 25 from the round 1 revision is where we mentioned that we are conducting research on sex biases in dispersal in a separate preregistration,

however we did not insert this information into the space use preregistration. The revised space use preregistration does not mention fitness or sex biases.

Comment 34: (R1) “Regarding dispersal syndromes, to us dispersal would refer to grackles moving out of the natal area when they are young and/or as adults searching for new territories. However, this type of longer-distance movement (and tracking of young birds) is beyond the scope of this investigation. Therefore, we are not investigating the effect of consistent behavioral differences in population dynamics.” While I agree with this answer at a detailed scale, the link is nevertheless made with evolutionary population dynamics through the study of three different populations at different stages of range expansion. Thus I still agree with the reviewer that dispersal / colonization syndromes are at play here, even if the variables investigated here are not directly dispersal – it seems implicit in the study design (otherwise, why compare these populations?)

Response 34: Our study is not designed to measure dispersal because we cannot track grackles over large distances and we aim to only study adults. Therefore, it is intentional that we do not refer to the movement behavior that we are quantifying as dispersal. While it is intuitive that range expansion follows from dispersal events, here in our second hypothesis we ask whether individuals from populations at different locations in the range show consistent differences in daily movement patterns. We think this is a valid question because individuals at the edge of the range may experience different social and ecological environments - both of which can affect daily movement behavior, survival, and fitness - compared to individuals in the core areas of the range. Results from this study may motivate future research comparing dispersal movements of juveniles or adults among these populations using technology that can track individuals over larger distances.

We have clarified this distinction in the new Introduction.

Comment 35: (R1) “but it is still unknown whether individual differences in exploration relate to daily movement patterns”: I’d replace this by “but it is still unknown whether such relationships rely on links between individual differences in exploration and daily movement patterns”.

Response 35: Thank you for this suggestion. We have actually deleted this sentence in the process of rewriting of our Abstract and creating the Introduction.

Comment 36: (R1) Response 30: even if there is no connectivity between the three study populations (which indeed does not seem plausible given the between-population distances!) I believe that the reviewer was thinking more in terms of connectivity between adjacent populations: if there are a network of highly connected populations, differences may disappear quickly. Maybe a word could be added here about whether many connected populations can be found around the study populations chosen here, or in other words whether the grackle populations form a continuous network of connected populations (even if dispersal occurs at a limited spatial scale). Also, was the discussion about turnover speed somehow evoked in the text?

Response 36: Thank you for your interpretation of connectivity - we were not thinking in those terms and we are happy to comment on this aspect. We examined the *Quiscalus mexicanus* species distribution on eBird.org

(<https://ebird.org/map/grtgra?neg=true&env.minX=&env.minY=&env.maxX=&env.maxY=&zh=false&gp=false&mr=1-12&bmo=1&emo=12&yr=1900-2011&byr=1900&eyr=2011>) and there is the potential for connectivity among all three field sites. However, connectivity between all three field sites is hindered by two geographic areas:

- 1) The Sierra Nevada mountain range between the Tempe, AZ and Woodland, CA field sites
- 2) The Sierra Madre mountain range and the high elevation central regions of Mexico between the Central American field site and the two US-based field sites

We do not know what effect these barriers might have on actual connectivity among populations because we are not aware of previous research that investigates this topic. We revised the preregistration as follows:

Hypotheses > H2: "... These populations are theoretically connected, however actually moving between two of our field sites within a few grackle lifespans is unlikely due to the large distances between field sites and two geographic barriers (the Sierra Nevada and Sierra Madre mountain ranges, and the high elevation areas of Mexico)."

Comment 37: Be careful not to use interchangeably neophobia and boldness, both traits have different definitions, as noted in the text: boldness includes a notion of risk to the individual while neophobia does not. They are usually considered two different personality traits for this reason. Boldness involves that individuals identify a specific risk before displaying a reaction, e.g. when a dummy predator is present.

Response 37: Thank you for pointing this out. We agree the appropriate term is "boldness" and so we made sure that we do not use "neophobia" in this preregistration or the g_exploration preregistration.

Comment 38: (R1) "Many studies that measure animal personality using novel objects have similarly used the same objects in two (or more) repeated exposures and found that responses are repeatable (e.g. @mccune2018personality). If there is habituation to the object because it has become familiar after Time 1, this will likely affect all individuals similarly and we will still be able to detect overall repeatability in behavior". While I agree with the first part of the statement (the use of the same object repeatedly on the same individuals in different tests, in most cases to make sure indeed the same level of stimulation / motivation is reached, as mentioned here), I am not sure that I agree with the end part: habituation to an object may differ between individuals – I would even say that it can be expected to differ between individuals! Yet, no ideal design for such tests exists (using the same object repeatedly vs. changing objects both have their drawbacks), thus I have no problem with using the same object in several tests, but I think it is necessary to acknowledge the limitation that this repeated use imposes.

Response 38: It is a good point that individuals may differ in habituation time. This could be a focus of a future study, but logistically we are not able to incorporate this into our current study. Therefore, it is reassuring to hear that you understand the non-ideal nature of our design. We have revised the preregistration to acknowledge this as follows in Methods > Summary of methods for measuring exploration:

..."Habituation may occur between time 1 and time 2, decreasing the novelty of the experimental setup. However, it is common practice to use the same setup across the repeated assays because it is very difficult to predict how threatening a novel object will be to a grackle, therefore if we accidentally introduce objects that are much more or much less threatening across the two time periods, this could obscure our ability to determine whether there are consistent individual differences with regard to these particular novel objects."...

Comment 39: (R1) "Based on these findings, it is unlikely that the aviary grackles that are released back to the wild change social groups or home ranges." Even if this sounds highly plausible, it remains necessary to formally show it by tracking individuals not held in captivity as mentioned just after.

Response 39: With our data it is impossible to know whether grackles change social groups after they leave the aviaries because they are not color banded and tracked prior to entering the aviaries (this is a consequence of the fact that we are not usually able to re-trap individuals). We think it is likely that social behavior and home range remain relatively similar because grackles caught in the same location are seen again together at that location. We can test whether time in captivity is related to subsequent group size to see if individuals that spent few to no days in the aviaries systematically vary in social behavior compared to grackles that spent a longer time in captivity. We added this to the Analysis Plan:

"We will additionally test whether time spent in captivity might alter the social behavior of grackles when subsequently released into the wild by testing maximum group size observed across each individual's focal follows as a function of the individual's captivity history (the number of days the individual was temporarily held in the aviaries before data collection on space use began)."

And we added the code for this model in Analysis Plan > Group size as a function of captivity history: `{r gsize, eval=FALSE, warning=FALSE, results='asis', echo=TRUE, include=TRUE} gsize = glm(Group ~ History, family = "poisson", data = data) hist(gsize$resid) summary(gsize)`

Comment 40: (R1) “It is possible that grackles that participate in aviary tests are more bold and exploratory than conspecifics that were never in the aviaries.” Why would it be so? Do you suggest that spending time in the aviaries may change the behavioural responses of the birds post-release? Or do you suggest that the birds initially placed in aviaries are not representative of the whole population, and if yes, why? Please can you explain?

Response 40: What we meant to emphasize here is that the birds that *remain* in the aviaries are the ones that participate in tests, and therefore are also likely a sample of the population that is relatively more bold. The birds that were brought into the aviaries, but refused to participate in the tests potentially fell on the shy end of the spectrum. However, because we needed to quickly replace these non-participants to maximize our sample size of aviary-tested birds, they were released before receiving boldness or exploration tests. We made sure to clarify this in our Response 18 (above).

Comment 41: (R1) “so that our question solely refers to adult behavior”: fine but large differences are usually reported (especially with regards to behaviour) between one-year-old and older adults, as mentioned by the reviewer. Because it is not possible to distinguish these two age categories here, as detailed by the authors, it could be good to mention this point clearly (to avoid further questions by future referees).

Response 41: Please see our Response 11.

Revision round #1

2019-12-23

Dear authors,

My apologies for the delay in handling the reviewing process of your pre-print ‘Does great-tailed grackle space use behavior reflect individual differences in exploration?’. Three reviewers have now read your pre-print, along with myself, and all of us found your planned study of high interest, as it should bring very important and relevant insights into the links between behavioural traits and space use in the wild, and ultimately help bridging gaps between individual behaviour and population dynamics in the context of range expansion and invasions. But as you will also see, we all have comments and suggestions on different aspects of your work, ranging from the conceptual part (do you really measure behavioural flexibility?) to the practical part (design of the measures of exploration and tracking in the field, including replicates of the three populations, explaining planned sample sizes, and statistical issues regarding measuring home ranges and including variables in your models). I think that all the comments and suggestions are highly relevant and I really recommend that you follow them as much as possible, since (as mentioned by reviewers) you are likely to face these comments for the manuscripts issued from the study once performed (and some may require adjusting your protocol / sampling from the start). Thus I think that these comments require such work on your preprint and thus would be happy to read a revised version of it.

My own comments below:

- I concur with the reviewers in that the question investigated here as it is stated currently relates to dispersal syndromes (i.e. consistent suite of behavioural differences between individuals) rather than behavioural flexibility (i.e. within-individual variation). Yet, as we understand, the authors plan to measure exploratory behaviour over a possibly large long of time (it is mentioned that individuals

may be held in captivity up to 6 months – see below regarding this point), and this may imply a series of measures on the same individuals over time, which should allow estimating within-individual repeatability in this behaviour and thus, by contrast, flexibility (i.e. the variable part). Similarly, the movements of tagged individuals can be followed in the field over large periods of time, which should allow estimating again repeatability and by contrast flexibility. However, we currently have no information about such estimates (how many series of measurements in captivity? how to estimate within-individual variability of movement in the field, over space and time?); instead, the feeling here is that basically only one measure will be used for each behavioural compartment (exploration in captivity and space use in the field, in particular with the use of a single measure of home range). I believe that, as presented here, the authors aim to address behavioural syndromes, but they nevertheless have the potential to explore flexibility, thus they should possibly re-consider their behavioural measures so as to make sure they estimate both the consistent and flexible part, and rewrite this estimate description and analyses parts with this in mind. I believe that assessing flexibility as stated from the start would certainly be of great interest here.

- In line with this, the authors should be careful about how they characterize exploration as measured by the tests in captivity and exploration as can be measured by space use behaviour in the wild. It is often assumed that prospecting movements represent exploration in the wild, but using the same term in both contexts here can be misleading about the hypotheses tested, as this gives the feeling that it is already assumed that space use is linked to exploratory – one of the very question investigated.
- Indeed, space use will be largely influenced by habitat use, thus I concur with reviewers that a clear description of the habitat available for different activities (foraging, breeding, mating...) is needed here for each individual monitored. If such information is not accounted for, it will be very difficult to address the questions of interest, especially if habitat varies globally between the three populations investigated.
- I also agree with reviewers that replicates for each zone would be needed to allow separating an individual population effect from the location within the expansion range. Alternatively, a more complete gradient of populations over the expansion range could also be used (e.g. either 2-3 replicates per population at the centre, middle and edge of the expansion range, or a gradient of 6-8 populations over the range, controlling if possible for longitude and/or latitude). I acknowledge that this may be practically difficult, but three points will likely be insufficient to fully answer the question of the link with population dynamics and expansion here.
- I do not know what the authors plan to do with the different measures of exploration in captivity, but rather than using different measures and link them one by one to the space use measures (which will automatically increase the total number of models and thus the risk of false positive), it may be better to first check whether and how these different measures relate to each other and whether they may define an overall exploration score for a given individual. I also concur with the reviewers' comments about (1) making sure about what is measured (as mentioned, the novel environment test could also be considered as a novel object test instead) and (2) it seems a bit far-fetched to assume that space use in the wild may be related to one or the other of the exploration measures in captivity only, as presented here (as mentioned, clear predictions about why it should be so seems rather difficult to do, especially without testing directly behaviour towards novel food sources) – assessing the relations between these different measures in captivity as a first step should allow addressing this point, and I would encourage the author to include such a phase in their approach, possibly simplifying prediction 1 alternatives 2 and 3 then here.
- Prediction 1 alternative 4 includes the first mention that only adult individuals will be tested: why is it so? This should be specified. I also concur here with reviewers in that even among adults, there may be large differences between yearlings (and possibly 2-years old, depending on the longevity of the species) and older adults in behaviour linked to dominance, experience etc. More information

should be given on this point, and also generally about the life-cycle and ecology of the species, as it is currently described nowhere in the pre-print. Yet, some of the assertions and hypotheses depend on such information. For instance Prediction 1 alternative 2 mentions different ecological constraints (habitats availability, predation, etc.) but it is currently very difficult to get an idea of the influence of these constraints. Similarly, whether grackles are territorial or live in social groups and to what extent (e.g. they may be flocking over the wintering season to find food but breed in individual territories) seems fundamental information to understand the space use patterns – and also the possible influence of captivity duration on subsequent behaviour after release (as clearly mentioned by reviewers, 6 months of captivity are likely to affect access to territory / social groups...)

- The reference to Duckworth and Badyaev (2007) study in Prediction 2 is misleading here as they worked on aggressiveness and not on exploration.
- Prediction 2 alternative 1: there could also be selection for certain phenotypes for other reasons than space use, e.g. on energy allocation trade-offs, that would in a second step, i.e. indirectly, impose constraints on space use. Maybe the authors should consider this possibility, at least theoretically (as it may be difficult to test it directly)?
- Overall, the link between the two main predictions is not sufficiently clearly explained, and more specifically, I do not really understand in what prediction 2 is addressing the main question, namely the link between exploration and space use. Of course, we understand that individuals will be sampled from the different populations over the expansion range, so that ultimately, the hypothesis tested is whether individuals from different populations differ in their exploration behaviour, which influences the expansion of the species. But to me, this should be more directly and clearly stated, to make the link between the two predictions clear; in particular the sampling scheme for capturing and testing individuals in captivity should be described. We only currently know that a total of approx. 60 individuals will be tested, but we do not know the composition of this sample in terms of population of origin, as well as age, sex, etc. See also the important comments by reviewers about sample size and how it is possible to make sure that this sample will be large enough (i.e. power analysis), especially if sex, age, population of origin etc. need to be accounted for.
- Again, more information is needed about the duration of captivity with regards to the experimental tests: why would 6 months be needed, and why should this vary between individuals? How many tests are performed per individual?
- Regarding the tracking protocol in the field: it is not clear to me how the authors will ensure that they can detect exploratory trips. How to make sure that there will be no bias towards already known locations, where birds may be searched for in the first place? Are there previous data about movement in this species that may help with designing search protocols? Or will experimenters search for birds until they are found (but in any case there will be a giving-up time point, and how will it be set up)? Also what is the distance of detection in this system with the tags used? This will influence the distance of approach needed for the experimenter, and thus its potential consequences on subsequent bird behaviour (e.g. will it flee if it detects the experimenter's presence?). The protocol mentions that the experimenters will not get too close, but I believe more precise information are needed on this point here (see also comments by reviewers on the comparison between tagged and color-ringed individuals, the latter requiring a relatively close approach for identification that may modify their behaviour differently compared to tagged individuals if detected from farther away; this comparison may also be influenced by the likely different resighting effort for the two categories). Also, information about tag mass with respect to bird mass should be given and justified. Overall, it will be necessary to describe the tagging and remote tracking procedure more precisely here.
- What is the maximum number of birds that can be expected to be monitored? The authors only mention 'as many as possible', but this will depend on the search effort in the field, and an estimate would be useful here. Also, what will be the relative effort of catching with each planned capture

method? Importantly, a potential bias in individuals' exploration behaviour depending on the catching method should be a posteriori checked using the behavioural estimates in captivity.

- Besides the comment by reviewers about the planned estimate of space use, I was wondering whether grackles could exploit successive home ranges, and if yes how this may be detected here? More generally, how will the end of the sampling period for remote tracking in the field be determined? Will it depend on each individual, based on his previous behaviour, or will it be a fixed period for all individuals? If the former, how to ensure that the same biological processes will be captured for all individuals (e.g. if some individuals may regularly move over a given range while others may exploit different home ranges successively)?
- Regarding independent variables: is a sex effect expected (and in this case why) or will sex be included only as a controlling factor here? The measure proposed for condition first surprised me, as I was expecting a measure of body condition such as the classical ratio mass / size (tarsus or wing length); then I understood that this is not really condition, but rather captivity experience, and I would suggest changing the term here so that there is no confusion. What about including a 'real' measure of body condition? and age? (see above and reviewer's comments). It would also be important here to first know which variables affect exploratory measures in captivity, so I believe that this should be a first step (probably included in the other protocol focused on these measures, but it would be important to mention it here as not all readers will also read the other protocols).
- Regarding the presentation: the list of variables in P1 alternative 1 could simply include the additional variables to avoid repetition. Among these new variables, the problem-solving performance is mentioned here but nowhere else! It would be important to explain why this variable is included here, what will be tested, etc.
- In the analysis plan section: how do you know that no data will be missing? How do you also know that GPS locations will be recorded during 'normal activities'? (besides, what is a 'normal' activity?)

This is a long list of questions and remarks, but I hope that the authors will find it useful to improve the presentation and justification of their study, and want to stress again that this is a very nice study plan that should provide many very useful insights about important questions, both on fundamental and applied points of views.

Preprint DOI: <http://corinalogan.com/Preregistrations/gspaceuse.html>

Reviewed by [Joe Nocera](#), 2019-11-13 16:54

This pre-registration outlines a study on whether behavioral syndromes (in this case, neophobia) are related to space-use in the wild, and by extension, to range expansion by Great-tailed Grackles. The study has been thought through very thoroughly, and the pre-study description here is well-written. I provide some thoughts and comments below that are either 1) meant to improve the delivery of the study, or 2) will be comments the authors will see again at some point. Despite my suggestions below, I think this is a great study, and the authors should move ahead with confidence!

1) In a way, it is nice that Prediction 1, and its Alternative 1, are mutually exclusive results. That means that no matter what the data say, there is a story to be told. As I was reading Prediction 1, my mind automatically went to the opposite, which is what you proposed in the Alternative. Nice job.

2) Under sample size rationale, I was hoping to see a more quantitatively-based rationale. You state that 57 is the sample size, but never really state why. Moreover, you never provide any assurance that this is statistically adequate. An a priori power analysis would be useful here.

3) Your radio-tracking protocol requires visual confirmation before data are collected. As such, the viewer will be within eyesight of the grackle at all times. I am not as certain as you are that this will not affect the bird's behavior. Can you provide citations to support this method as having no effect?

4) My biggest complaint in the entire study is around your use of Minimum Convex Polygons as the metric of home range size. MCPs are notorious for overestimating home range size. And where you are collecting very fine-scale data at the GPS level, it seems odd that you would use such a coarse metric for home range. At the very least, you should consider doing one of the Kernel Density methods (especially AKDE, seeing as you are looking at autocorrelation anyway). Or Brownian Bridges. MCPs are simply not matched to the scale of the data you are collecting.

5) What about the habitat the birds are using? Should this not be inventoried and used as an independent variable to help explain home range size? Without it, you are assuming that home range size is directly related to neophobia and exploration, and that all habitats are created equal. And that is certainly not true. Could more exploratory grackles be better at defending prime territories? Or worse at it, because they move around too much? I think that ignoring habitat and focusing solely on behavior is a misstep that may limit you later on.

I wish you the best of luck in this study!

Reviewed by [Marion Nicolaus](#), 2019-10-22 16:43

[Download the review \(PDF file\)](#)

Reviewed by [Laure Cauchard](#), 2019-11-26 18:13

The goal of this project is to examine the role of a personality trait (exploration tendency) on space use in wild-caught great-tailed grackle.

- Be careful with the term 'behavioural flexibility' (see Audet J-N, Lefebvre L. What's flexible in behavioral flexibility? *Behavioral Ecology*. 2017;28(4):943-7). If you follow the real definition of behavioural flexibility (from psychologists), an exploration task is not appropriated. Behavioural flexibility is measured through standardized tests of reversal learning, set-shifting and self-control to determine if animals are able to rapidly and efficiently adapt to different situations. An exploration task measures only the propensity of an animal to explore a novel situation.
- Measuring exploration: 1) Novel environment: a tent is placed in the middle of the aviary (familiar environment). Even if it is a novel environment inside the tent (which is transparent), it seems to me that this test looks like a novel object test. Moreover, the performance to this test is measured as the latency to approach to 20cm of the tent, or the closest distance. They do not enter the novel environment? So they are not exploring the novel environment. 2) Novel object: the food is still close to the novel object, you are not measuring exploration but neophobia, as you are not measuring attraction for novelty but the motivation to feed despite the novelty (the center of the aviary is not that far from the end of the aviary when the food is). I would use a different novel object for Time 2 of this test. The latency to approach to 20cm of the novel object, or the closest distance, is a good measure for neophobia.
- Measuring space use: the protocol to determine home range size from radio-tagged birds seems ok to me. What about the protocol for the other birds?
- Are the birds released at the same place they have been caught?

- I think it is a good idea to measure space use for grackles that stayed in the wild, to control for the possibility that grackles that were previously in the aviary have different space use behavior from non-aviary-held grackles after their release, as they can stay in aviaries for a very long time (6 months) and they may have been forced to find a new territory, or find a new social group (it is a social species). A good sample size would be required here to rule out this possibility.
- Statistics: I think you should control for age, if you can, even if you use adults only. What is the average lifetime of these birds? 1 year-old adults might differ in their space use and/or exploration level vs older birds.

Author's reply:

[Download author's reply \(PDF file\)](#)