Eurasian lynx populations in Western Europe: What prospects for the next 50 years?

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Submitted by Sarah Bauduin 19 Jan 2022 10:17

Abstract

Persistence of viable populations may be uncertain for large carnivore species, especially for those established in human-dominated landscapes. Here, we studied the Eurasian lynx in Western Europe established in the Upper Rhine metapopulation (i.e., Jura, Vosges-Palatinian and Black Forest populations) and in the Alpine population. These populations are currently considered as endangered or critically endangered due to high anthropogenic mortality and isolation. We assessed lynx persistence over a 50-year time horizon by implementing a spatially-explicit individual-based model while accounting for road mortality and habitat selection. Forecasts showed a steady growth rapidly reaching a stabilization phase with high resident female occupancy for the Alpine and Jura populations, and a positive growth for the newly re-established Vosges-Palatinian population. Moreover, this population showed a difference in female occupancy between the northern part, where a recent reintroduction program was conducted in the Palatinate Forest, and the southern part. Only the group of individuals in the Black Forest had an irregular growth probably due to the small number of only male lynx at start of the simulation and poor connectivity to surrounding populations. Exchanges of individuals between populations were limited, the Jura population playing the role of a crossroad. Persistence of lynx in Western Europe seems likely on a large scale over the next 50 years. However, lynx persistence in the southern part of the Vosges-Palatinian population and in the Black Forest appears challenging without long-term conservation management.

Keywords: Lynx lynx, population persistence, spatially-explicit individual-based model

Round #1

by Elodie Vercken, 22 Feb 2022 11:43
Manuscript: **https://www.biorxiv.org/content/10.1101/2021.10.22.465393v2.article-info**

Recommendation under minor revisions

Dear Authors,

Thank you very much for submitting your work for recommendation in PCI Ecology. Your manuscript has been evaluated by two reviewers and myself, and we all concur that it is of excellent quality. The topic (prediction of long-term demography of a large carnivore in Europe) is most engaging, both on the scientific and social dimensions. The impressive amount of data, the level of details in spatial modelling, and the very clear and detailed description of modelling methods were all acknowledged as major strengths of your work, which has the potential to be of interest to a wide community of ecologists and conservationists.

I would be most happy to recommend this work for PCI Ecology, provided you can address the minor concerns raised by the different evaluators, in particular:

- A few more details seem to be necessary on the different regression models used to build the collision and habitat layers, and on the evaluation of breeding territories

#1.Bauduin et al.: We answered Henrik Andren's comments regarding these points (answers #31, #32, #26).

- The discussion could use a couple of clear conclusions on the factors most critical for population growth and expansion, at present it is difficult to understand clearly why the population fails to colonize the entire available habitat

#2.Bauduin et al.: We have recalibrated the model since the first submission, thanks to Henrik Andren's precious comment on collision probabilities regarding the resident and dispersing individuals (hence the long delay since the first submission), and with the new model, simulation results have changed and we modified a lot the previous discussion. However, we tried to highlight, as much as our understanding on the population mechanisms goes, the factors most critical for population growth and expansion (lines 449-451, 493-496, 499-502, 518-523*).

*Line numbers for this comment and the following refer to the manuscript version with the visible track changes.

- Some perspectives on the potential evolution of the landscape: agricultural lands vs forest covers, new road or infrastructure projects, key dispersal routes, …

#3.Bauduin et al.: We answered Hector Ruiz's comment regarding this point (answer #15).

Don't hesitate to ask if any of the reviewers' comments are unclear to you, or if I can help in any way. I sincerely hope our comments are helpful to you and contribute to improving the manuscript further.

Review by Elodie Vercken

The manuscript is very clear and well-written. I appreciate the fact that the main text was kept short, with all necessary details in appendices. I reckon there might need just a little more on the structure/logic of the model in the main text, if one wants to get a general idea without referring at all to the appendices (for instance, one large figure to summarize how it works, especially the part on habitat selection, which is the trickiest).

#4.Bauduin et al.: We moved figure A.1 in the main text (lines 228-236) and we added a few lines to better describe the individual-based model structure (lines 204-220).

The main result is that population sizes stabilize quite quickly, although favourable habitat does not seem saturated. So dispersal capacities clearly seem like the limiting factor here. It would be interesting to have some perspectives on the expansion speed observed after the different reintroduction events mentioned lines 145-149, and compare with the predictions that are made. Is the environment less permeable now?

#5.Bauduin et al.: We recalibrated the model since the first submission, thanks to the comment from another reviewer about the use of the collision probabilities regarding the resident and dispersing lynx, and with the new model, simulation results have changed. We do not observe the population stabilization with places not saturated at the end of the simulation like before (Figs. 3, 5 and 6) and we adapted the discussion.

However, regarding lynx expansion speed, we find it difficult to quantify it as it may vary a lot, as well as depend of what we are looking at (e.g., establishment of an individual, a couple, a population; signs of reproduction; etc.). However, we tried to put into perspectives, as much as our results allowed us, the recolonization of the population in Western Europe as observed with the simulation results (lines 423-437, 500-503, 518-523).

I found it hard to understand why some large chunks of perfectly good habitats are not occupied (e.g., the southern part of the Vosges population). The discussion seems to point degraded functional connectivity, but it is not obvious when looking at Fig 4 where breeding habitat seems continuous across the Vosges area. Maybe adding the main barriers to the plot would help visualizing things. Indeed, my main concern is that I was impressed by the quality of the modelling and the data, but a bit frustrated that I failed to understand fully the dynamics at work here. A few summary statistics on the model outputs might help: proportion of males/female individuals that die during dispersal ; the average distance/duration of the dispersal phase ; average life span ; proportion of individuals killed by collisions; etc…

#6.Bauduin et al.: With the recalibrated models, simulation results have changed (Figs 5 and 6).

Concerning the summary statistics, the calibration and validation phases of the model (Appendix C) provide new results such as dispersal distances and number of collisions. We also added in the Results, a lynx density map (Fig. 6).

I might have missed it, but I did not see any sensitivity analysis, which maybe could also help understanding better why the population does not manage to expand and fill the available habitat?

#7.Bauduin et al.: We added a sensitivity analysis (Appendix C), using results from the model calibration. Also, population predictions have changed with this new calibration and individuals managed to expand and fill all the available habitats with the recalibrated model (Figs. 5 and 6).

One of the major strengths of this model stands in the highly detailed spatial layers for collision risk and habitat quality, but there are a few things that I did not understand :

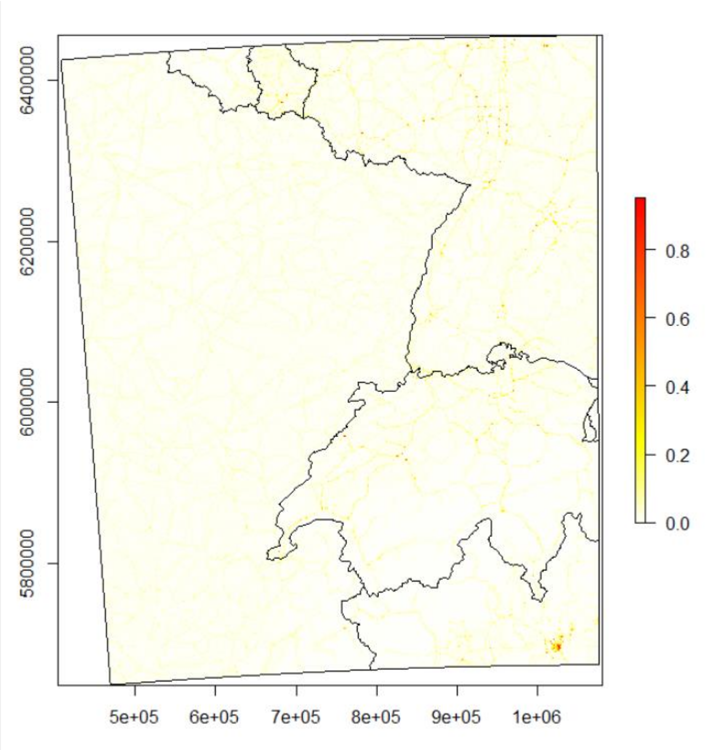
- what is the quality of the regression model for collision risk ? How much data was it fitted with

#8.Bauduin et al.: The dataset we used represented 84 lynx-vehicle collision events recorded between 1982 and 2016. We added this information in Appendix A (lines 887-888).

- Collision risk for residents is calculated as the mean risk over an individual's territory: don't you think it gives enormous weight to high-risk roads that might be avoided by individuals in practice? The collision risk seems huge to me, but it is difficult to infer on Fig A2 because the colour scale is all red from 0.01 to 1 (please adjust the colour scale •).

#9.Bauduin et al.: We did not model lynx movement inside their territory and we do not know how they use this space regarding the roads. We chose to add a spatial mortality as the mean collision risk inside their territory to still include a collision risk as some roads intersect lynx territories. Not including any collision risk would have not been realistic as lynx move across their territory in which roads and the risk of vehicle collision exist. Adding a mean collision risk was a way to include this risk. We did not have any information, to our knowledge, to include this risk in another way that could better represent the reality. However, if resident lynx do not evenly use their territory regarding the presence of roads, this can bias the resident mortality. We added this information in the Discussion concerning the limit of the model (lines 571-578).

We purposely chose this color scale adjustment to obtain a map showing some road network. As most of the collision probability values are smaller than 0.1, using an even color scale (here is an example) did not seem relevant.



"Collision layer" with collision probabilities between lynx and vehicles estimated between zero and one with an even yellow to red color scale.

- I am also not sure I understood the habitat layer model correctly: lynx presence data from France are used to evaluate the influence of different landscape or habitat elements. But the lynx population in France was quite small, so the absence of individuals at a given location does not imply that the habitat is unfavourable? Further details on model fitting might help here (maybe a map of the area used for model fitting, relatively to the area in which habitat quality was extrapolated?)

#10.Bauduin et al.: We used a multi-year occupancy model to create the habitat layer. We used lynx regular presence data in France from 1994 to 2017. Even if we did not use lynx presence data from the whole study area to which we predicted the habitat layer, using 23 years of lynx presence data in France provided a dataset large enough to correctly estimate the model. Moreover, we feel environmental conditions in Germany and Switzerland were similar enough to those in France to be able to predict lynx occupancy and then derived habitat types over our entire study area without bias.

The occupancy model we used is based on detection/non-detection data (*Louvrier et al. 2018. Mapping and explaining wolf recolonization in France using dynamic occupancy models and opportunistic data. Ecography, 41(4), 647–660*). An estimate of the surveyed area (i.e., sampling effort) was computed each year regarding the number of trained observers in the area and their circle of prospection (https://ecologicalstatistics.shinyapps.io/flexdashboard_effort/). The model used lynx detection and non-detection data only from surveyed cells. Once estimated, the model was applied over the whole study area. We completed the model explanation (lines 929-931)

Fig 4 : which cells are represented? Only breeding habitat with >0 occupancy? The legend should be clearer, also it might be interesting to visualize favourable habitat that is not occupied at all.

#11.Bauduin et al.: Colored cells were cells that were included in a female territory in at least one simulation replicate. White cells (territory occupancy equal to 0) were cells never included in a female territory across all 100 simulations replicates.

We changed the map color scale as well as highlighted cells of breeding habitat that were never included in a female territory. We also completed the figure legend according to your comment and the new map (Figs. 5 and C.1).

Reviews

Reviewed by Hector Ruiz, 07 Feb 2022 14:46

This is a very interesting article on predicting long-term persistence of Eurasian lynx (*Lynx lynx*) populations in central Europe. The article is very well written and clearly explained. I know SE-IBMs but I am far from being an expert and despite this, I was able to perfectly understand everything that has (and has not) been done and included in your model. All the details to make the model as realistic as possible (which should always be the main goal of predictive models) have been considered and taken into account. I have some thoughts/reflexions about some of the model limitations (most of which have already been explained by you in your manuscript) particularly regarding not having considered landscape and land use changes along your prediction time of 50 years (please see my comment below). Of course I agree with you that if you could have included data on poaching and genetics the model would have provided more realistic results. Sadly, that data is generally hard to obtain and thus difficult to incorporate in the models. Taking all this into account, I think that you have done a great job using what was available to predict the persistence of lynx populations in Central Europe. I think your article is very useful not only from the lynx ecology and conservation point of view but also to scientists and conservationists as a tool to run future SE-IBM with other species and in other environments. Congratulations! Everything looks fantastic so only a couple of minor comments and some reflexions are included.

#12.Bauduin et al.: Thank you very much for the kind words and your constructive comments which we answered in details below.

L46: I would avoid the use of the word "viable" in your abstract. Persistence and viability are different concepts with different implications in ecology and your model would probably fit better with the concept of persistence (see my next comment).

#13.Bauduin et al.: We agree. See our answer to next comment (#14).

L122: Persistence or viability? I think these concepts are greatly different. A population may persist with very bad genetic quality and very low population numbers; however that population may not be viable from a long-term perspective. As you are not including key viability components in your model (illegal mortality or genetic characteristics) I would probably talk about persistence and remove the word viable from the abstract as it may sound confusing.

#14.Bauduin et al.: We agree. We avoided using the word "viability" in our manuscript for this reason but this mention of "viable" in the abstract slipped by our attention. We removed the word "viable" from the abstract (line 47*).

*Line numbers for this comment and the following refer to the manuscript version with the visible track changes.

L684 (Impact of Land Cover): I think your methods to determine the influence of land cover on lynx occupancy are fantastic. However, did you consider modelling habitat modification along the 50 year period to assess the effects on viability of lynx populations? I see in L1014 that you did not include variations in landscape in your model. For example, one scenario may be that agriculture intensification continues growing and thus gaps between lynx populations get larger consequently complicating its viability. You explain in your introduction that habitat fragmentation is one of the main threats for lynx worldwide and thus these changes would be expected to have great implications. Another possibility would be that forest cover increases (as it may be the case in many areas of Europe), and thus connectivity among lynx populations would increase. Could you please explain why you did not use this approach? (model complication, lack of evidence, etc)? Land change across Europe in the last 50 years has been substantial and it is thus expected that something similar occurs in the next 50 as it has not been otherwise explained in the text. From a conservation (and prediction) point of view I think that considering the future changes in the European landscape inside and around lynx populations would make your predictions much more realistic, particularly when knowing that fragmentation can greatly impact lynx populations.

#15.Bauduin et al.: We agree that changes in the landscape will greatly affect population persistence. However, we did not have a readily-available landscape model to predict our environment on a 50-year horizon and moreover, some hypotheses would have been necessary on certain landscape components (e.g., change in agricultural pressure, urban/road development, lynx management actions). Therefore, numerous scenarios could have been defined. Moreover, the fact that our populations are distributed over three countries, with each one having their own politics in landscape management, many combinations of different scenarios per country could also have been defined.

One or two scenarios could have been tested but they would have not represented a more likely future landscape than another scenario or our static landscape. We therefore chose to use a scenario "as is" for simplicity.

Besides, the model seemed already complex enough to explain and the manuscript long enough. We did not want to add more analyses (i.e., scenario creation, model running, and result evaluation) in this already complex manuscript. Our predicted lynx results are according to a static environment, which on a 50-year horizon does not seem completely unrealistic to us. Of course, it is one version of the future in this landscape. Other predictions for lynx persistence would be made in a different landscape. We stressed that point a bit more in the Discussion (lines 579-585).

L691: Remove one "used"

#16.Bauduin et al.: We removed it (line 932).

L815: Change "kitty" for "kitten"

#17.Bauduin et al.: We changed for "kitten" (line 1544).

Reviewed by Henrik Andren, 15 Feb 2022 07:45

I think this is an important paper forecasting lynx occupancy in different regions in Western Europe. The paper is easy to follow. The appendix and model description are very well structured and follows Overview, Design concepts, and Details (ODD) protocol.

#18.Bauduin et al.: Thank you very much for your review and the time you took for all your comments. We answered each one in details below.

However, I have a problem to understand how the "breeding habitat" in habitat layer (Figure A3) can result in the occupancy layer (Figure 4). To me there is a miss-match between the two. Most of my questions are related to the differences between these two maps.

Black Forest and Vosges-Palatinian regions have the largest areas of continues "breeding habitat", whereas both Jura and Alpine have very fragmented "breeding habitat". But the modelling results in higher occupancy in Jura and Alps than Black Forest and Vosges-Palatinian.

#19.Bauduin et al.: Detailed answer below (#21)

Firstly, I wonder how female territories were established. A dispersing female establish a territory if she is in "breeding habitat" and the is enough unoccupied "breeding habitat" around she current position. The territory core area is 43.5 km2 in the Alpine region and 73 km2 in the other populations (from page 45, lines 885-900).
Must all the territory core area be "breeding habitat? If so, there are lots of small fragments of "breeding habitat" in Jura and Alpine regions that will never be occupied (Figure A3), as the fragments are smaller than the territory core area. If not so (i.e., the territory core area can contain other habitat types), how much of other habitat types (dispersal or matrix) can the territory core area contain?

#20.Bauduin et al.: The territory core area is only composed of "breeding habitat". However, the shape of this core area does not have to be a circle, cells only need to be connected one another by at least one cell. Isolated fragments of "breeding habitat" smaller than a core area cannot be part of a territory, unless at least one cell connects this small fragment to another one to make a bigger continuous patch. We better explained this process in the ODD (lines 1514-1519*).

*Line numbers for this comment and the following refer to the manuscript version with the visible track changes.

If the territory core area can only be "breeding habitat" then it is very surprising that Black Forest and Vosges-Palatinian have a very low occupancy (Figure 4) and that Jura and Alpine have much higher occupancy.

#21.Bauduin et al.: We recalibrated the model since the first submission, thanks to your very precious comment (#23), and with the new model, simulation results have changed.

In Figures 4 and C1 it is not possible to evaluate if recorded paths of female are also found outside “breeding habitat”.

#22.Bauduin et al.: We agree it is hard to see if recorded paths are found outside “breeding habitat” in figure 4 but the zoomed areas on figure D.1 are big enough to show that most of the paths seem to be in “breeding habitats”.

As a reminder, any cell that is colored (not grey nor white) on the female occupancy map is part of a female territory and therefore is of “breeding habitat” as only this type of cell composes the female territories.

On Figure 5, recorded paths are shown only for a general view to see that there is no recorded paths in large “white” or “grey” areas (i.e., in an area where no simulated female lynx established their territory over the 100 simulations).

On Figure D.1, with the zoomed areas we can see that most of the recorded female locations (nodes of the lines) are in “colored” cells that represent “breeding habitat”, but mostly in cells colored in yellow-red representing cells often selected by simulated females to establish their territories.

Some recorded locations may fall in white (non-breeding habitat) or grey cells (breeding habitat cells never selected in a female territory for accessibility reason, patch size, etc.) as we cannot see clearly where all the nodes fall. But the overall message was a general visual validation to see that most of the recorded paths of females in the field are located in area where simulated females often established their territory.

We added some details in the Methods (lines 271-274) and Appendix D (lines 1847-1851).

My second major question deals with the “collision layer” (Figure A2) and how the collision probabilities are treated for resident and dispersing individuals.
Resident lynx suffer from a fixed baseline mortality (0.1; Table B1) and a spatial one derived from the collision layer (between 0 and 1) and the risk is on a yearly time step.
Dispersing lynx follow a daily time step also with a fixed mortality (0.0007; Table B1) and a risk of collisions. A daily mortality risk of 0.0007 correspond to a yearly mortality risk of 0.23 (1-(1-0.0007)^365), which is a reasonable yearly mortality. I estimated the population growth rate with the fixed mortality and reproduction given in table B1, but without the “collision risk”, to about lambda = 1.25 (a realistic growth rate).
However, how is the collision risk layer used? Is it the same collision risk for residents (yearly time step) and dispersers (daily time step)? If so, the collision risk is very much higher (maybe unrealistic high) for dispersers than for residents. If not so, how is the collision risk estimated for the residents vs. dispersers? How is the collision risk estimated for a disperser moving several steps?

#23.Bauduin et al.: Thanks to this very important comment we added two correction factors for the collision mortality: one for the resident individuals to increase the value from the collision layer to transform it into a yearly mortality, and another one for the dispersing individuals to decrease the value from the collision layer to transform it into a per step mortality. These two correction factors have been calibrated with data (Appendix C). This model calibration is the reason for such a long delay since the first submission but it was so important for the results.

If residents (yearly time step) and dispersers (daily time step) have the same collision risk (but for very different time steps) then it can explain the very low occupancy of Black Forest and Vosges-Palatinian regions, although these areas have large continuous breeding habitat. The low occupancy can be explained by the very low probability of colonization of these areas (or very high collision risk for dispersers). The occupancy map (Figure 4) seems to be entirely a result of the "random initial population" (Figure A4) and dispersing between regions are almost impossible because of the very high collision risk. The number of successful establishments in non-native populations is very low (the cumulative number over a 50-year period is less than 2 for all regions; Figure 3). Is this extremely low establishment in non-native populations supported by data?

#24.Bauduin et al.: Results have changed with the recalibrated model and this comment does not really apply anymore.

Page 11, line 225, Page 14 lines 265-266, and Page 17 line 288 – The populations go towards a stabilization phase indicating a carrying capacity. I should call it "saturation" instead of carrying capacity, as it is a result of "all" female territory core areas are occupied ("saturated"). I think it would be very interesting to report the population size (divided into females and males) at the stabilization phase for each region, as population size is more important for long-term persistence than occupancy and growth rate.

#25.Bauduin et al.: We replaced "carrying capacity" by "saturation" (lines 405-406).

At first, we produced Figure 2 as the number of individuals in each population. We finally changed it for the current figure presenting the population growth. We feel that growth rates are better indicators of population persistence instead of population size as a small increasing or stable population has a better chance of persistence than a large decreasing population. Moreover, the public debate around the lynx presence in Western Europe, and large carnivores in general, is always driven by numbers, with too-big or too-small populations (Trouwborst et al. 2017. Interpreting 'favourable conservation status' for large carnivores in Europe: how many are needed and how many are wanted?). We did not provide population size to avoid putting numbers that could be interpreted without taking into account all the model assumptions. Finally, the model has many assumptions and reality simplification, especially on the initial populations for which we do not have a clear idea of the actual number of individuals, in particular for the large Jura and Alpine populations. The actual number of lynx initially created drives a lot the resulting number at the end of the simulation, whereas it has a lesser impact on the population growth direction, as this parameter is a relative value compared to the initial populations. We feel it was less biased to present population growth in the results instead of population size.

I also wonder about the fairly low occupancy reported for Jura and Alps (pages 14-15, lines 265-274; Jura = 0.45, Alps = 0.60). I wonder if this can be explained by the many small fragments of "breeding habitat" that are too small for a territory core area? It would be very interesting to know the maximum number of female territory core areas that can fit into different regions. What is the maximum possible occupancy (can it be 100 %), given that the fragment of breeding habitat has to be larger than the female territory core areas? This question is also related to the question above if a female territory core area can include also other habitat types (not only "breeding habitat" but also "dispersing habitat" and matrix).

#26.Bauduin et al.: Results have changed with the recalibrated model and we feel this comment does not apply anymore.

How are the different regions (or "populations") delineated outside the core area (Figure 4)? For example, the "breeding habitat" west and northwest of the Jura and Vosges-Palatinian regions in Figure 4 are continuously getting more and more fragmented without a clear boarder. The regions ("populations") are spatially defined as one report occupancy for each region, but it is not described how the regions are spatially defined.

#27.Bauduin et al.: The population layer was defined using lynx presence data. The process to delineate the population areas is only mentioned in the legend of figure A.4 "Each cell of the gridded study area was assigned the population from its closest cell of lynx regular presence" (lines 1011-1012). We better describe how this layer was made in the Appendix and its use (lines 1000-1004).

Can the model forecast important dispersal routes? It would be very interesting to report the routes that successful lynx have used, although there are very few of them. The dispersal routes in the SE-IBM might be very informative (better than for example circuitscape models).

#28.Bauduin et al.: The model can indeed forecast dispersal routes and can be a great tool to evaluate functional connectivity. We did not show a map of dispersal routes nor perform any connectivity analysis for two reasons.

First, the model seemed already complex enough to explain and the manuscript long enough. We did not want to add a connectivity analysis (with a different literature, more results, and a discussion on connectivity) to the viability analysis we already performed.

Second, one of the major limit of this model is the inclusion of roads only a mortality source and not as movement barriers. Simulated lynx do not "see" roads when they disperse, the move through them without resistance and either live or die regarding the collision risk (i.e., spatial mortality) of the cell. To perform a relevant connectivity analysis, the simulation of this process needs to be improved to include roads as movement barriers.

Page 19, lines 339-341 – Lynx males settle and stay even without females (Samelius et al. 2012, J. Zool. 286: 120-130), but they move over very large areas (Aronsson et al. 2016). Thus, I fully agree that a more realistic rule would be than male stay in areas also without females. But hopefully the results are not sensitive to this rule.

#29.Bauduin et al.: The simulation of male settlement is a simplified version of the reality as it is only based on female presence. Therefore, without available resident female, no dispersing male can ever settle down. We know this can bias population predictions, especially for those where a few or no females were present at the start of the simulation. We mentioned this in the discussion for the Black Forest, as it may have impacted the predictions for this population in particular (lines 474-480).

Page 21, line 391 – Herdtfelder 2012 is not in the reference list.

#30.Bauduin et al.: We added the reference (lines 759-761).

Page 34, lines 667-668 – Is it possible to report the exact model for the “collision layer”? I guess it is a logistic regression and it would be interesting to the have the coefficients (intercept, total road length, type of road of the longest road segment and proportion of urban area) to be able to apply the “collision layer” in other study areas.

#31.Bauduin et al.: We added a table with the parameter estimates for the best model identified to explain lynx-vehicle collision (lines 912-914).

Page 36, lines 697-699 – Is it possible to report the exact model for regular lynx presence? I guess it is a logistic regression and it would be interesting to the have the coefficients (intercept, presence of agricultural fields, forest and open land, distance to highways and human density) to be able to apply the “lynx habitat layer” in other study areas.

#32.Bauduin et al.: We added a table with the parameter estimates for the best model identified to explain lynx presence (lines 953-955).