Dear Managing Board of PCIEcology,

We are grateful for the feedback received on our article entitled **Identifying drivers of spatio-temporal variation in survival in four blue tit populations**, from two reviewers and a PCIEcology recommender. We have revised our manuscript by carefully considering all the comments received, and you will find below a detailed record (in blue) of all the changes made accordingly.

We hereby resubmit our revised version of our study, and look forward to your final decision regarding a recommendation.

Please note that all data files and models used in this manuscript are shared online in the bioRxiv submission. We have also added a Conflict of Interest Disclosure section in the manuscript.

All authors know and agree of this submission to PCI Ecology.

On behalf of all authors of this manuscript,

Best regards,

Dr Anne Charmantier

Round #1 // Authors' responses

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by Dieter Lukas, 2021-03-01 12:19
Population variation in blue tit survival

Dear Authors,

Your preprint entitled "Identifying drivers of spatio-temporal variation in survival in four blue tit populations"has now been reviewed and the reviewers' comments are appended below. As you will see, both reviewers consider your study to be sound and insightful, and I share their views. Yet they have several comments that need to be addressed carefully before I can recommend your preprint.

// Thank you for these appreciative comments.

In particular, I agree with both reviewers that more detail should be provided in the manuscript to explain the potential links between the factors you investigate and survival. I think this will make the manuscript clearer and help readers to see how your findings might transfer to other populations or other species. From my perspective, as someone who does not know a lot about your study species of blue tit, I think it could also help to have a paragraph in the introduction that briefly explains some key parameters of the species as they relate to survival (e.g. seasonal breeder, non-migratory but swarm forming in the winter?, when do individuals of which sex disperse how far?, is the highest mortality in the winter, during incubation in the nest, during feeding from predation?, what is the maximum longevity?). Having this information might help to explain better in the introduction why you chose these various factors and how they could potentially shape survival in the different populations. In turn, I think it would help if the introduction is focused only on those factors that are central to your study: for example, the abstract mentions boldness which has no direct relation to your study setup.

// We have extensively revised the introduction according to these comments: the paragraph of introduction starting in L97 now offers a more detailed biological background of the species, as well as of survival studies in this species (with around ten additional references). We have removed the mention on bolder personalities in the deciduous habitat, although this was in the framework of describing the difference in pace-of-life between the two habitats, which allows to make predictions on survival rates. We have clarified this prediction at the end of the paragraph.

I have an additional comment about the presentation of the approach and results in the tables and figures. There is a lot of information, but it is sometimes difficult to understand what information there is to extract for someone not as familiar with the setup as you.
Table 1: Is this supposed to be a supplement? It currently appears at the end of the manuscript, and you later focus on the more specific models rather than presenting the full breadth of results from all the models.
// Table 1 should be retained in the main text of the manuscript. Its format being very large and not easily amenable to insertion within the main text (because of its landscape format), we have placed it at the end of the ms, but we can easily insert it earlier on in the results section. To reduce the amount of information provided in the main text, we have however moved Figure 3 to the appendices (now Figure S1).
Table 3: There are some formatting issues in the pdf. I also wonder whether you want to set the number of digits after the decimal points (e.g. have four digits) to make comparisons easier.
// We are sorry about the formatting issues that arose when we saved the previous submitted version in a pdf format. Also, we apologize that some references to tables were erroneous (e.g. Table 4 was cited as Table 3 in the sup mat). We have now solved these issues, and we have also chosen to restrict the number of decimals for Deviance and ΔAICc to 2 in all tables, while survival and recapture probabilities, P-values and R^2, all have 3 decimals now. In response to Ana Sanz-Aguilar we also provided beta estimates associated with temporal covariates for models including all study sites (i.e., table 3 and table S4).
Table 5: I think it would be interesting to have your results here as well for comparison. You could also add a column that explains whether each site is deciduous or evergreen.
// We have added our results here in a last row, although we provide the full range which 'hides' differences due to habitat heterogeneity.
Figure 1: Could you maybe include photographs that illustrate the forest conditions at the four sites?
// It is a nice suggestion to witness the difference between deciduous and evergreen forests, we have now included two pictures as illustration of the difference in habitats.
Figure 2: The label for the fourth population E-Muro in red is missing. Maybe you could combine this figure with the additional illustrations of year-by-year variation shown in Figure 3 and Figure 4a.
// We apologize for this, the figure was cut in the pdf, we have now made sure that the legend is embedded in the figure and will not be cut off.
Figure 3/4a: As mentioned above, the year-by-year trends on their own are not particularly informative. I think they gain their information from the comparison with the other trends, to compare the extent of variation in each and whether yearly fluctuations might align.
// We find it useful to illustrate the environmental variation, however we agree that it is not essential for the main text, hence we have moved Figure 3 as an Appendix 3 (now Figure S1). Combining Figures 2, 3 and 4a in a single figure would not fit on one page.

Reviews

Reviewed by Ana Sanz-Aguilar, 2021-02-19 12:25
The manuscript "Identifying drivers of spatio-temporal variation in survival in four blue tit populations" analyzes four long term databases to understand the temporal variations in survival

probabilities in relation with environmental conditions and density dependence. The scientific background is sound and the methods are robust and correctly implemented. I'm very surprised with the discrepancies with the previous analyses of Grosbois et al. The authors have made a good job re-analyzing the same time window to understand the discrepancies, but again results are different. As the only difference is the removal of experimental birds from the database, is it possible that these birds could be more affected by environmental conditions for any reason? (I recognize that I find this explanation weird but I have no alternative suggestions). In any case, I think that the current analyses is better conducted that the one of Grosbois (I think that removing experimental birds is the correct decision) and the databases are longer and thus more suitable to explore factors affecting the temporal variations of survival. As a general suggestion I recommend the authors to check the beta estimates of covariates to be sure if the effect is positive or negative (if the 95%CI do not include zero) and to provide R square values (the percentage of temporal variance explained by covariates) for all the analyses.

// We thank the reviewer for this evaluation of our work and for the positive comments. Regarding the discrepancy with Grosbois et al, we are equally puzzled even after the comparative analysis presented in Appendix 3. Although we used broadly the same analytical framework as Grosbois et al., there are still differences in the handling of the dataset, and in the modelling that may marginally affect the results (e.g., Grosbois et al. used a Sex+Pop*Year model for recapture probabilities, whereas we used a sex*pop model). But these differences are probably insufficient to explain the differences in findings in our reduced dataset. We agree with the reviewer on the potential role of experimented individuals in these discrepancies and the hypothesis that « birds undergoing experiments are sensitive to climatic conditions in a different/stronger way » was added in the discussion (L504).

Regarding beta estimates and R^2 values, we added them to Table 3 (i.e., main covariate analysis), Table S4 (i.e., additional analysis based on the same study period and study sites as Grosbois et al.) and to the main text when necessary.

Specific comments:

Figure 2. E-Muro is lacking in the Figure legend. I recommend to specify that model 18 include the effects of "age+pop.year" in survival.

// We apologize for the legend missing, the figure was cut in the pdf, we have now made sure that the full legend appears. We have also added now the information on the survival fit in model 18 as suggested.

Line 25. I suggest to indicate that populations "can" display lower survival. This is true for blue tits but may differ for other species/populations. As this is a general statement I suggest including the word "can" or "may".

// We have rephrased using "would".

Lines 26-27. Maybe the authors could indicate "adult blue tits" or "breeding blue tits". As age class is included among the effects tested it seems without further information that the analyses could deal also with juvenile survival, which is not the case.

// Line 28 this sentence clearly states that the analysis in on "adult survival" hence we do not think there can be a confusion here on the fact that survival from fledgling stage to breeding stage is not studied.

Line 93. Please could you indicate in brackets the age classes considered?

// We have added this information in brackets, although it was already detailed in the methods section.

Line 114. Please could you summarize the mechanisms provided/suggested by Grosbois et al to explain survival variation in Mediterranean populations of blue tits as a function of Sahel rainfall? How this index could influence climate in the Mediterranean is neither explained in methods (line 167)

// We have done this, the text now reads (L127) : "In particular, adult survival was correlated with both local-scale weather conditions (summertime and wintertime index combining rainfall, temperature and wind variables) and a large-scale tropical index in early summer: rainfall in the Sahel. The authors noted that the Sahel rainfall index could represent either a tropical influence on European weather, or be related to local climate in a way that is not captured by their local summer climate index."

Lines 199-204. Population density index. Sorry I cannot understand how the index was calculated. Only the next boxes present all the years were considered (e.g. 26 in E-Pririo) or different number of nest boxes were considered for different years?

// We are grateful for this comment since the description was indeed confusing. We have rephrased this paragraph and hope it is now clearer.

Line 213. I suggest changing "censored right" by "right censored"

// Modified as suggested.

Line 226. It should be Fig 4b instead Fig 3b.

// Thank you for pointing this out, there were several typos with table and figure references, we have carefully gone through all of them. Here it was in fact Table 3, and on the next line, it was Table 4 rather than Table 3. Also, figure 3 has now been moved to the Appendix, which has shifted once again the figure numbers.

Line 255. I think that model selection should be the same for all the covariates, not using the AIC for breeding density and the p-ANODEV for the others. I suggest to use all of them and discuss them at the light of R2 value that indicates the percentage of temporal variation explained by the covariate and finally (when there could be doubts) the authors could check the 95% CI of the beta estimate corresponding to the covariate slope to check if limits include zero.

// In response to this comment, we modified the text in the Methods and Results sections to clarify and homogenise the inference approach. The inference is primarily based on model comparison (AICc). ANODEV were performed for temporal covariates to examine the extant of time deviance explained by each covariate (we used ANODEV for all temporal covariates, not only large scale ones). In response to this and another comment, we also included the beta estimators. The conclusions remained unchanged. With the main (complete) dataset, beta values confirmed a weak trend in the summer MOI covariate with a negative beta (-0.064 [CI95 -0.117;-0.012]).
With the reduced data set, winter MOI was the only covariate that significantly reduced the deviance of the model. Both winter MOI and SRF had significantly non-zero beta estimators (table S4) but model comparison suggests that the effects of the large-scale time covariates are overall quite small.

Table 2. Here recapture probability P should be in capital letters to be consistent with the general notation in the manuscript.

// This has been corrected, thank you for spotting this.

Line 298. It should be Figure 3, instead Figure 3A.

// Thank you for spotting the typo, the figure number has now changed.

Table 3. Why the model Phi (age+pop+q_winterMOI) is not included?

// We apologize for this mistake. Model Phi (age+pop+q_winterMOI) is now presented in table 3 (mod 79)

Line 351. I recommend checking the 95%CI of the beta estimate to be sure that population density had a negative correlation with survival.

// Thank you for this suggestion. We have included beta estimates in the text. Both are negative. One is significant (E-Pirio), the other not (E-Muro).

Line 449. Include the reference Blondel et al. 1992 after "see Table5".

// This reference was added as suggested.

Line 463. I think that here, as breeding density was not significant via ANODEV test it would be better to discuss the percentage of temporal variation explained by this covariate and also the 95%CI of the beta estimate (see previous comments).

We now provide detailed results (including p-anodev and beta estimates) in the Results section as suggested, and we mention the low percentage of temporal variance explained by density in the discussion. In both populations (E-Pirio and E-Muro), the relationship between density and subsequent survival is negative. Although this link seems closer in E-Muro (with R2=23%), the beta estimate of the model is significant only in E-Pirio. This discrepancy might be the result of large differences in sample sizes and number of years between the two populations (19 years for E-Muro and 38 years for E-Pirio).

Reviewed by Vicente García-Navas, 2021-02-28 11:51

This study relies on an impressive dataset (almost 40 years of study), which has allowed us to better know this species, the blue tit, and gain insight into key aspects within the field of Evolutionary Ecology, such as local adaptation or phenotypic plasticity. Some studies derived of this long-term research program are frequently included as textbook examples of adaptation to environmental heterogeneity, and exemplifies the peculiarities of the Mediterranean region. Prof. Anne Charmantier has taken the baton from the renowned Prof. Jacques Blondel and now she leads the team. The Montpellier group continues to produce high-quality science and contribute to the blue tit being considered the "lab rat" of field studies in Evolutionary Ecology.
In this study, Bastianelli et al. use Capture-Mark-Recapture modelling to investigate the effects of

climate (at both regional and local scale), breeding density, sex, and age on adult survival in four blue tit populations of Southern France. Overall, I find the study clear, concise and well executed, and the methodology is sound and solid. In my opinion, the manuscript is generally clearly written and appropriately and thoroughly referenced; very minor language editing would be helpful throughout.
// We are grateful for these positive comments on the manuscript and on the long-term study.

My comments are generally minor and offered more to stimulate discussion than being critical. Despite the results are negative (no effect on climatic conditions on survival probability), I think this is a nice contribution, and the authors should move ahead with confidence.
I only have some minor points which could help to further improve this paper:

Specific comments:
Page numbers missing.

// Page numbers were added.

Abstract:
L23 Habitat "naturalness" sounds odd. I'd use level of anthropogenization or something similar instead.
// We refer the reviewer to this paper which provides a review of the concept of habitat naturalness: https://academic.oup.com/forestry/article/85/2/293/529315 . Any phrasing using the anthropogenic influence on habitats would make the sentence more awkward, in our opinion.

L24-25 I would say that 'populations whose individuals…' as talking about the behavior of a population as a whole is somehow controversial. Populations do not exhibit behavior syndromes, individuals do.
// This sentence was rephrased so that it is the individuals and not the populations that have higher reproductive investment and bolder behaviours.

L38-39 Please, provide the (potential) reason for this decline. It is not clear if these two populations belong to the same habitat type (e.g., evergreen forest) or locality.
// As explained in the discussion (paragraph starting L520), our analysis suggests that this decline is not linked to the direct meteorological variables (temperature, rainfall) explored in this study. We provide in this discussion ideas on what could be explored next to understand this decline, but it is all very speculative. Hence in the abstract, we have added "calling for further investigation to explain this decline" to avoid speculations in the abstract. Another option would be to remove this sentence altogether.

Introduction:
L46 Please, add Oxford (serial) comma after "trends".
// Done.

L66 I would add a few examples of species or populations with strong density-dependent effects on their dynamics.
// We have added here two references: the Gamelon et al 2017 study and also a sentence explaining results in blue petrels (Barbraud & Weimerskirch 2003).

Material & Methods:
L198 The number of nestboxes is rather low in all the studied populations in comparison with other studies in which the number of boxes typically oscillates between 80 and 100. I am just curious about the mean occupation rate and the size of these woodlands (i.e., the number of breeding pairs per ha)

(I am sure these details are given in previous studies carried out by the team but I think this info is appropriate for the purposes of the present study). In addition, besides occupation rates, it would be interesting to know if these (concrete?) nestboxes are used by other species -e.g., great tits, crested tits, nuthatches, rock sparrows-, with which blue tits compete for nesting places (cavities). Also, it would be interesting to know if nestboxes are protected against potential predators (snakes, weasels, woodpeckers) and if it -predation rates- constitutes a negligible/anecdotal factor or not at a population level.

// Thank you for these interesting comments. The total number of nest-boxes in these study areas was in fact not provided in the methods. The confusion probably arose because of the 'Population density index' section which discusses the estimation of population density in a restricted area of each site (now rephrased). The density of nestboxes is indeed lower than in some other sites which offer nestboxes typically at 5 to 10 times the natural nesting densities. The key information here is that our nestboxes are "neighbouring boxes are 50m apart" (L156). Following this important comment from the reviewer, we have added a whole methods paragraph providing more information regarding the number of nestboxes, the sites areas, the breeding density and the protection against predators, although note that these protections of nestboxes are more likely to influence nestling survival than adult survival.

L238 examined instead of "tested".

// Changed as advised.

Results:

Fig.1: color coding for one locality (E-Muro) is missing. I find this figure a bit crude (too Excel-like) and a bit of elaboration would be more than timely.

// I think this comment refers to figure 2, which had been cropped during the pdf creation. We have rectified this, changed the position of the legend, and have removed the outer line around the figure to make it less 'Excel-like', although we are not sure what is wrong with that.

L291-293 Intriguing. I wonder if this is related to differences in sex roles during the breeding period between habitats (e.g.; higher male provisioning effort in evergreen forests).

// This is an interesting hypothesis for which we unfortunately have no data to test it. We have pondered upon the importance of discussing sex differences in this study. Since it is not one of our main questions here, we have removed the mention of survival differences between males and females in the last paragraph of the discussion (since the past literature did not allow to make a clear-cut prediction) and have chosen not to discuss this point further.

Fig. 3: I would superimpose a Generalized Additive Model (GAM) in each panel, which would allow to derive a trend across time (if any). I think this time series analysis would be more informative than the raw data.

// This figure has now been moved to the Appendix as Figure S1. The purpose here is to illustrate the year-to-year variation, and since there is no significant temporal trend, we have not added the trends on the figure.

L336 Suggestion: "[…] which differed between the Corsican (E-Pirio, D-Muro, E-Muro) and the mainland (D-Rouviere) populations".

// Thank you for this useful suggestion, which we have followed.

L325. I would include a figure to illustrate the observed negative linear trend in survival in Rouviere and evergreen-Muro.

// Temporal variation in survival rates are illustrated in Figure 2. We attempted to add the temporal trends to D-Rouviere and E-Muro on this graph, but it makes the figure more confusing. We feel that the trend can already be witnessed in this figure.

L340 remaining populations?
// In fact, this statement is true for the four populations. We have attempted to clarify this by splitting the sentence in two.

L342-343 This sentence is a bit misleading for the reader. Could you reformulate it a bit?
// This section was reformulated.

L343-343 Suggestion: There was found a linear temporal trend for population breeding density in the populations located at Muro.
// This section was removed for simplication.

Discussion:
L405-406 I agree with this explanation. However, it has been shown that parents contributions to brood care may vary across populations. Some studies have found that female blue tits feed their young less frequently than their mates regardless of the habitat type (evergreen or deciduous forest) (e.g., García-Navas & Sanz, 2012. Condor, 114: 612-621).
// Thank you for pointing this out, we have added the reference and mention that this provisioning roles can shift across populations.

L410-415 On this regard, I would be interesting to know if there are differences in terms of immigration rates (i.e., breeding adults not ringed as chicks in the focal population) among localities in order to know if different source-sink dynamics between the four study sites and the surrounding natural populations (birds breeding in tree cavities) may play a role in explaining the observed variation in recapture probabilities. I think authors may refer here to previous studies in which the studied sites are thoroughly described (e.g., Blondel et al. 2006, BioScience, 56: 661-673).
// Thank you for this remark, indeed, immigration rate is lower in D-Rouviere, we have now stated this, with an appropriate reference.

L424 Now, I think my previous comment on nest predation rates is especially opportune.
// You are right, and now readers know that the sparrowhawk is one of the main adult predator.

L463 Authors indicate that the effect of breeding density on adult survival was only detected in the two evergreen populations. However, they do not provide a rationale to explain this finding. It is a bit disappointing as (IMHO) the authors have enough information based on decades of work in this study system to discuss more in depth about why the effect of density is particularly noticeable in this habitat type (e.g., different local conditions: lower availability of food resources; larger foraging distances and territory sizes, etc.). Furthermore, I wonder if nestling mass determines survival probability in these populations. Do chicks fledge in worse conditions in sclerophyllous forests? If so, does nestling condition have a significant impact on survival? For instance, in a study with great tits, Rodríguez et al. (2016; Ecology & Evolution, 6: 4458-4467) reported that large and early chicks have a greater first-year local survival probability. In the same population (located in a Mediterranean environment, orange groves in Valencia), Greño et al. (2008; Journal of Avian Biology, 39: 41-49) suggested that post-fledgling survival increased with mass, and decreased with temperatures during the nestling period.
// We appreciate this comment and have extended the discussion here with references to past work that indicates higher constraints for parents, and potentially higher breeding competition, in evergreen forests(L477 and onwards). We have not developed on nestlings since our study is only on

adult survival.

L468-470 This is true, however I think authors could easily provide more details about: i) the density of nestboxes per ha, ii) the density of boxes occupied by blue tits per ha (I would expect a lower density of breeding pairs in the evergreen forests), iii) the density of boxes occupied by other competitor species per ha, iv) the average number of nests predated per year in each population, and v) the number of immigrants recruited in each population per year. This info would be very helpful in order to better understand the different local conditions to which blue tits must face in each of the four study sites. Thus, I suggest including a table with these five descriptive parameters for each population if possible.
// Thank you for this suggestion. All these parameters are not adequately estimated, e.g. there is discussion around whether all unringed birds should be considered as immigrants, especially in areas where natural cavities are available within, or very near, the focal study site. We have however now provided information in the methods on the area covered by the study sites, the total number of nestboxes, and the range of breeding densities over the years across the whole study area (L156-L170).

L503-515 This result is striking as one would expect a decline linked to a particular habitat type (evergreen or deciduous) or locality. However, authors only found this pattern in one of the two localities at Muro, and the two localities displaying a decreasing linear trend belong to different habitat types (E & D)! This certainly makes it difficult to draw any kind of conclusion.
// As you say, the decline does not seem habitat-specific. We have added this in this paragraph, and agree with you that this makes the interpretation very speculative, hence we do not wish to extend it more.

Conclusions (last paragraph): Instead of highlighting the main drawbacks of the study, I would try to highlight its strengths. I think authors should try to improve the “home-take message”. I found this last paragraph a bit vague; this study comprises a unique dataset and I think it deserves a better corollary.
// Thank you for this constructive comment. We have rephrased this last paragraph to bring a more positive conclusion and take-home message.

Hopefully some comments will be useful to further improve the manuscript. Good luck with the peer-review process.
// Thanks again for all these comments that have improved our manuscript