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Reply to the comment on "Synchronizing biological cycles as key to survival under a scenario of global change: The Common quail (*Coturnix coturnix*) strategy" by Rodriguez-Teijeiro et al.

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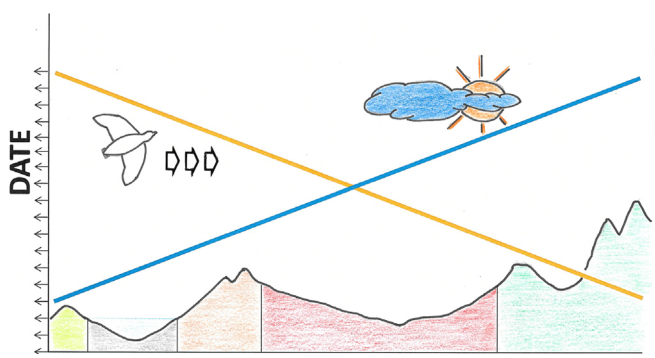
HIGHLIGHTS

- The ecological modeling of migratory species is of great scientific interest due to the threat of global change
- Geographic spatio-temporal models constitute great improvement compared to local models for understand ecological strategy
- Space-time use with climate can help to understand biological synchronization process under global change scenarios

GRAPHICAL ABSTRACT



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ABSTRACT

Two methodological criticisms of our paper "Synchronizing biological cycles as key to survival under a scenario of global change: The Common quail (*Coturnix coturnix*) strategy" (Nadal et al., 2018) were proposed in the comment by Rodriguez-Teijeiro et al. (2018) regarding: 1) our estimates of the mean date of arrival, duration of stay and departure stages in the different regions studied; and 2) the analyses carried out to correlate the phenology of the species with changes in the climate variables. The conceptual model that we presented relates the dynamics of this quail population, which moves between short periods of stays, and the spatio-temporal structure of their geographic distribution data, in order to understand the ecology of these birds and to link their movement and residency patterns with geographical area and climate conditions. The probability that quail are resident in a region on any particular date is a result of their overall ecological strategy. We believe that Rodríguez-Teijeiro et al. (2018) have misunderstood our model, leading to their criticism of the statistical tests that we applied.

1. Introduction

We thank Rodríguez-Teijeiro et al. (2018) for their comment on our recently published model (Nadal et al., 2018) to explain the survival of Common quail (*Coturnix coturnix*) with regard to the effects of global change. The overall response to our paper has been positive and highlights the interest in our model as a tool for understanding the successful strategy of a migratory bird. We accept that our model is provisional in nature, however its superior capacity to explain the strategy of Common quail compared with previous hypotheses represents a major step forward in the understanding of the biological cycle of this species. Here,

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we address the misunderstandings of Rodríguez-Teijeiro et al. (2018), and set out to clarify the use of our conceptual model and the accompanying statistical tests. We shall address each of their criticisms in turn.

2. The estimates of the mean dates of arrival, stay and departure

Rodríguez-Teijeiro et al. (2018) disagree with our method of estimating the mean dates of arrival, stay and departure in the different regions studied. In our opinion, they have misinterpreted our scales of spatial and temporal distribution and interpreted our model in an unduly narrow way. Our estimates of the mean dates of the three temporal stages (arrive, stay, departure) were made in the same way, and their confusion may have arisen from their interpretation of the mean dates in the different geographic areas. We used a broad interpretation of the data to understand differences between the geographic areas in relation to the model. All of our observations are underpinned by our theoretical framework, which deliberately used broad units of space-time. It follows from this that there will be a considerable number of local exceptions; for example we would not expect to find that every member of the quail population inhabiting a particular geographic area experiences exactly the same conditions. Within a single geographic area, slightly different conditions would prevail from site to site, although the average conditions would be representative for most of the quail inhabiting that area (Urban et al., 2016). To date, population studies have dealt with average values for the population considered and individual exceptions are accommodated within these averages (Alroy, 2015; Fauchald et al., 2017). The individual exceptions confirm the rule because they are not sufficient to unbalance the mean and so mask the underlying correlations (McDonald, 2009).

Our conceptual model does not compare geographical areas or separate nearby geographical areas, but only structures the geographic data in order to understand quail ecology. Rodríguez-Teijeiro et al. (2018) claim that the quail in any one stage would only be engaged in a single activity, for example breeding. However, our conceptual model is much broader and assumes, for example, that during the stay stage most, but not all, individual quail are breeding. The fact is that during the stay stage not all quail are breeding because all animal populations include floaters, non-breeding animals that may be considered surplus to the population (Payo-Payo et al., 2018). Contrary to their arguments, at the end of this stage fewer quail are ringed in southern areas because birds are unavailable for capture for a variety of reasons: some quail have finished breeding; some are breeding in irrigated land or at high altitude; some have already moved on; some are non-breeding floaters; and some are sedentary.

They believe that a strict interpretation of the date of ringing should be possible because accurate information on each ringed quail should form a part of the ringing record. Clearly this would be desirable, but unfortunately this level of information is not available at present because dataset have not this information. Our model was created using the information currently available to us in an attempt to obtain the best possible understanding of the ecology of this species. A model based on a broad interpretation of the data, dealing with averages rather than specific individuals, was required because of the complex dynamics of the quail population and its distribution across the three stages (Post and Forchhammer, 2002). Rodríguez-Teijeiro et al. (2018) assume that it is possible to analyze the data specifically for individual birds, for example at the departure stage, but this would require that each quail simply leaves the place where it was ringed. In practice, while most quail begin their return migration at this time, many make short movements elsewhere in any direction before migrating and only some simply move directly south. One cannot assume that any one bird necessarily starts its return migration directly from the place where it was ringed, or that it always follows a direct route south. Our model avoids these difficulties by focusing on averages, and on solid data regarding the date and geographical region of ringing (Post et al., 2009).

Our conceptual model summarizes the complex dynamics of movement and short stays within the quail population as a whole. The stages (the time component) can be associated with the geographic regions used (the space component) by the probability of quail presence. The idea is simple and robust: the probability that quail are observed on any date, in any region, is a result of the strategy of this species. The model is methodical, clear, unambiguous, rigorous, coherent and precise, and rationally systematizes and correlates the available information.

3. Relationship with climate variables

Rodríguez-Teijeiro et al. (2018) complain that they could not access the original data used in our model (Nadal et al., 2018). Without repeating our analyses using the estimated values from these data sets, we can only reply to this criticism in general terms. As we explained in the methods section of our paper, the datasets are available at several different organizations (see Nadal et al., 2018). While we did list the sources consulted, a detailed description of the complexities of the data and their use in our conceptual model was beyond the scope of a methods section without increasing the length of the paper unduly. As a result, limited understanding of the crucial contextual information allows the potential for erroneous assumptions and interpretations of the data we extracted (Mills et al., 2015). For example, Rodríguez-Teijeiro et al. (2018) claim the existence of collinearity between climate variables and the regions studied. Collinearity arises when one predictor (variable) in a multiple regression model can be linearly predicted from the others with a substantial degree of accuracy. In our study we worked with simple regression models where collinearity is not possible because only one predictor is involved (McDonald, 2009). In addition, their misunderstanding of the conceptual model is amplified by its transfer to the statistical model, leading to further misconceptions and confusions born of the initial misinterpretation. Their first error, concerns the geographic information used in the model. Each region is defined by its geographical coordinates (latitude, longitude), its height above sea level (altitude) and its characteristic climate. As we move over the Earth we change regions, coordinates, altitude and climate. Because migration constitutes movement through various regions in search of optimal resources for life, our goal is to understand migration within a global change scenario. Our conceptual model is spatio-temporal and links geographic region and date as a single variable to synthesize geographical and habitat information (Alexander et al., 2018; Godsoe et al., 2017).

Second, they confuse scale considerations between locality and region with altitude differences between localities in different regions. Rodríguez-Teijeiro et al. (2018) speculate that one cannot associate these differences with climate changes between regions. However, the association between climate, altitude and geographic region is a clear example of the synthetic function of the conceptual model (Raudsepp-Hearne and Peterson, 2016). Their argument becomes incoherent when they point out that the regions are associated with particular climates and then say that the date differences of quail presence are only due to the differences in altitude between localities, and finally conclude that one cannot associate temperature with the date of quail presence.

Table 1
Regression models between average quail dates, and rainfall and temperature for the Ebro Valley region. (N) Sample size, (b ± SE) slope ± standard error, (R^2) coefficient of determination, (F) F-statistic, (P) probability of type I errors.

Model	N	b ± SE	R^2	F	P
Arrival date and arrival precipitation	30	−0.04 ± 0.06	0.01	0.36	0.55
Stay date and stay precipitation	32	0.32 ± 0.12	0.19	7.01	0.01
Departure date and departure precipitation	21	−0.08 ± 0.23	0.01	0.12	0.73
Arrival date and arrival temperature	30	−1.90 ± 2.56	0.02	0.55	0.47
Stay date and stay temperature	32	−4.82 ± 1.97	0.17	5.99	0.02
Departure date and departure temperature	28	6.70 ± 5.55	0.05	1.46	0.23

They propose separation of the geographic variable into several analytical units, and this may well be a good idea if we had sufficient data for more detailed modeling (Schneider, 2001).

We need to very cautious in extrapolating from the conceptual model to a statistical model and must consider whether the database is sufficiently robust to allow such comparisons with acceptable levels of error (Wright, 1992). Their arguments fail at several levels: a) they have not analyzed the original data, and so could not have performed the filtering and treatment processes necessary to obtain a quality database without biases, errors or misinterpretations; b) they have not considered that the subdivisions they propose would risk increasing the probability of type I and type II errors, given the resulting substantial decrease in the size of the dataset (to one eighth of its original size); and c) their multiple comparison increases both error types to such an extent that the statistical test loses its internal logic. In fact, the probability that they calculate multiplies the results of the comparisons which give the adjusted-p eightfold (multiple error effects are accumulated and overwhelm the logic of our statistical treatment). For example, following the reasoning of Rodríguez-Teijeiro et al. (2018), it makes more sense to decide to analyze only the geographic region with the largest dataset (the Ebro Valley region) and not to make multicomparisons with the other regions, since the reduction in the sample size proportionally increases the risk of type II errors (Benjamini and Hochberg, 1995). Reducing the quantity of data in this way produces very similar results to the original analysis obtained using all of the data (Table 1) and provides no support for Rodriguez-Teijeiro's suggestion. Therefore, our previous results are upheld.

4. Concluding remarks

In our opinion, the arguments put forward by Rodríguez-Teijeiro et al. (2018) to improve our understanding of how Common quail synchronize their biological cycles to improve their survival under a scenario of global change are invalidated by their lack of understanding of the database we used and of the conceptual model which we produced. Their accumulated misinterpretations of our conceptual model and resulting inappropriate statistical model have been applied to a body of data that by its nature could not support their conclusions. Their confusing interpretation of our conceptual model and misunderstanding of our statistical logic fail to shed light on the understanding of the effects of global change on the Common quail, rendering their arguments inappropriate to the rigorous analysis of the data presented in our paper.

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