



# Which temporal resolution to consider when investigating the impact of climatic data on population dynamics? The case of the lesser horseshoe bat (*Rhinolophus hipposideros*)

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**Which temporal resolution to consider when investigating the impact of climatic data on population dynamics? The case of the lesser horseshoe bat (*Rhinolophus hipposideros*).**

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***Application for Oecologia Highlighted Student Paper:***

*Determining the temporal resolution of climatic variables when identifying their impact on wild population abundance is a rising concern. Our work proposes a way free of most assumptions for doing it.*

Author Contributions: OF and JB provided count data. ELT and AB developed methodology.

PLJ, PLG, SJP and EJP analyzed the data. PLJ, PLG, SJP and EJP wrote the manuscript.

## Abstract

Climatic variables are often considered when studying environmental impacts on population dynamics of terrestrial species. However, the temporal resolution considered varies depending on studies, even among studies of the same taxa. Most studies interested in climatic impacts on populations tend to average climatic data across timeframes covering life cycle periods of the organism in question or longer, even though most climatic databases provide at least a monthly resolution. We explored the impact of climatic variables on lesser horseshoe bat (*Rhinolophus hipposideros*) demography based on count data collected at 94 maternity colonies from 2000 to 2014 in Brittany, France. Meteorological data were considered using different time resolutions (month, life cycle period and year) to investigate their adequacy. Model averaging was used to detect significant predictors for each temporal resolution. Our results show that the finest temporal resolution, e.g. month, was more informative than coarser ones. Precipitation predictors were particularly decisive, with a negative impact on colony sizes when rainfall occurred in October, and a positive impact for June precipitations. Fecundity was influenced by April weather. This highlights the strong impact of climatic conditions during crucial but short time periods on the population dynamics of bats. We demonstrate the importance of choosing an appropriate time resolution and suggest that analogous studies should consider fine-scale temporal resolution (e.g. month) to better grasp the relationship between population dynamics and climatic conditions.

## Key Words

*Rhinolophus hipposideros*, temporal resolution, model averaging, climatic variables, population demography.

## Introduction

Weather and climatic conditions have a great influence on the population dynamics of most species (Kingsolver 1989; Saether et al. 2004; Forrester and Wittmer 2013). Climatic factors directly impact organisms, especially in cases of extreme climatic events (Şekercioğlu et al. 2012; Leigh et al. 2015). They also affect species' dynamics by altering their environment (Peterman and Semlitsch 2014; Akesson 2016; Hasan and Ansari 2016; Ceglar et al. 2016). Because of their great impact on species at the bottom of the food chain, weather conditions are also known to have a drastic impact on food availability (White 2008). For these reasons, the abundance and distributions of species are expected to be altered in the current context of global climate change (Thomas et al. 2004).

In this context, understanding the impact of climatic factors on population dynamics and demography appears to be fundamental to interpret or predict long term population trends (McLean et al. 2016; Urban et al. 2016). This topic has been studied for many species, generally using long-term observed abundance or other population dynamics metrics based on count or capture data at one particular moment in the life cycle of the species. These data are then modelled as a function of weather, considering mainly temperature and rainfall, but sometimes including other variables (Bruggeman et al. 2015; Kerbiriou et al. 2015; Bleho et al. 2015; Kanno et al. 2016; Dugger et al. 2016). Obviously, variables included in the model directly depend on the considered species biology, but more surprisingly, the temporal resolution considered is also highly variable. The latter citations correspond to recent studies that deal with various taxa, and all of them have used climatic databases offering a monthly (if not daily) resolution. Monthly resolution involves a great number of climatic variables. In a few cases, the number of variables were reduced by pre-selecting months based on preliminary analysis (Parent et al. 2016) or on expert knowledge (Kerbiriou et al. 2015). Most studies have aggregated climatic data to correspond to climatic seasons (varying from two to

73 six month periods) that are consistent with the life cycle of the species of interest (Bruggeman  
74 et al. 2015; Bleho et al. 2015; Ciuti et al. 2015; Kanno et al. 2016; Dugger et al. 2016;  
75 Masciocchi et al. 2016; Townsend et al. 2016). Occasionally, studies even considered these  
76 data by averaging them over a year (Nouvellet et al. 2013). Another option is to mix different  
77 time resolutions in the same models, such as in BIOCLIM derived models, which include 19  
78 variables that are aggregated on a yearly, seasonal or monthly (extreme month) basis and are  
79 now commonly used to predict species distributions (Barbet-Massin and Jetz 2014; Del Toro  
80 et al. 2015; Beltramino et al. 2015; Ray et al. 2016). The absence of clearly defined criteria to  
81 select the temporal resolution is problematic (van de Pol et al. 2016), particularly for  
82 population dynamic processes, because the temporal resolution considered when studying  
83 these processes can greatly affect the outcome of statistical or predictive models (Radchuk et  
84 al. 2014).

85         Bat populations are particularly sensitive to climatic variations, and are recognized as  
86 valuable indicators of climate change (Jones et al. 2009). For example, in temperate regions,  
87 cold temperature will greatly reduce their food availability, e.g. the abundance and activity  
88 level of insect prey (Hoying and Kunz 1998; Ciechanowski et al. 2007). Inclement weather,  
89 including heavy rain, will also increase the energetic cost for flying and maintaining  
90 euthermia, and will reduce the efficiency of echolocation (Reiter 2004a; Burles et al. 2009).  
91 Furthermore, numerous studies have demonstrated the impact of climatic conditions on the  
92 activity, survival, and reproductive success of bats (Adams and Hayes 2008; Burles et al.  
93 2009; Schorcht et al. 2009; Frick et al. 2010; Adams 2010; Amorim et al. 2012; Lučan et al.  
94 2013; Amorim et al. 2015). Climate change during the last decades has already caused a shift  
95 in the distributional range of some bats (Uhrin et al. 2016; Wu 2016), a process that will  
96 probably be exacerbated during the next decades (Rebelo et al. 2010).

Studies of bat population dynamics usually take into account weather as one of the fundamental explanatory variables. Those studies are mainly based on counts or captures made at one particular moment in the life cycle, such as during parturition or the hibernation period (Grindal et al. 1992; Zahn 1999; Hoyle et al. 2001; López-Roig and Serra-Cobo 2014; Kerbiriou et al. 2015). Climatic factors usually include rainfall and temperature, which can be the daily mean (Zahn 1999; Schorcht et al. 2009; Kerbiriou et al. 2015) or minimum temperature (Grindal et al. 1992; Hoyle et al. 2001; López-Roig and Serra-Cobo 2014). Some other variables, such as drought severity, winter severity or winter duration, can also be included, using different proxies (Schorcht et al. 2009; López-Roig and Serra-Cobo 2014; Amorim et al. 2015; Kerbiriou et al. 2015). Once again, the time resolution of these variables differs between studies, and climatic factors can be considered for specific months (Grindal et al. 1992; Zahn 1999; Kerbiriou et al. 2015), averaged over seasons consistent with the species biology (Schorcht et al. 2009; Frick et al. 2010; Adams 2010; López-Roig and Serra-Cobo 2014), or averaged over even longer periods (Hoyle et al. 2001; Amorim et al. 2015).

The lesser horseshoe bat (*Rhinolophus hipposideros*) is a small insectivorous bat of recognized conservation concern (Bontadina et al. 2000). This bat forages exclusively in woodlands, preferentially in dense areas (Bontadina et al. 2002; Reiter 2004b), and is already considered as a good indicator of biodiversity loss (Haysom et al. 2013). After the last glaciation, this species expanded its range from southern Europe to northern parts of Europe (Dool et al. 2013), into environments with colder and less stable climate (Bontadina et al. 2000). In spring, females leave the underground sites used as hibernacula and gather in maternity roosts, which are generally in warmer places, like attics, and the parturition and rearing of offspring takes place during June and July. Mating then occurs principally between the end of September and the beginning of the hibernation period (Gaisler 1966). The life cycle and activity of *R. hipposideros* are particularly affected by weather conditions. This bat

prefers higher temperature for its maternity roost than other attic dwelling species (Kayikcioglu and Zahn 2004). However, if available, they will switch to colder satellite roosts if temperatures become too high during summer. These observations suggest direct effects of weather on the thermoregulation and energy budget (Kayikcioglu and Zahn 2004; Seckerdieck et al. 2005). Inclement weather (i.e. cool and wet) before parturition generally delays birth and decreases the average size at birth and growth rate of the juveniles. These effects are explained by energetic costs, implying more torpor and a slowed metabolism for pregnant females, as well as by decreased food availability (Reiter 2004a). However, the global effect of weather conditions on the overall population dynamics of *R. hipposideros*, crucial information for understanding population trends, is not documented (Bontadina et al. 2000).

As climatic impact can greatly differ depending on the level of response considered (McLean et al. 2016), we investigated two proxies of the dynamics of *R. hipposideros* colonies: colony size, which is the result of the dynamics of colonies, and fecundity, one parameter that drives these dynamics. In order to understand the impact of climatic conditions on these parameters, we used count data from 94 colonies (Brittany, France) collected by local associations during fifteen years. These count data offer reliable estimates of colony size as confirmed by independent non-invasive Capture-Mark Recapture methods (Puechmaille and Petit 2007). Brittany populations are at the species range margin, and thus not at their optimal climatic conditions, a situation where population dynamics are likely to be strongly influenced by the weather (Thomas et al. 1994; Geber 2008; Bateman et al. 2011). Furthermore, this region is under a temperate climate greatly influenced by oceanic conditions, and the weather can be very variable during and between years (Lamy and Dubreuil 2010). Our study had two objectives: 1) investigating the temporal resolution at which climatic variables should be considered when assessing the population dynamics of a

bat species at a regional scale and 2) improving our understanding of the climate impact on a species of great conservation concern. Because most climatic databases facilitate access to data with at least a monthly resolution, we considered a monthly resolution, a several months resolution (corresponding to life cycle periods that are suitable for *R. hipposideros*), a yearly resolution, and also mixed temporal resolutions that correspond to commonly used BIOCLIM variables to explain variability in colony size and fecundity in *R. hipposideros*. We hypothesized that finer temporal resolution would better grasp weather effects.

## **Material and Methods**

### **Monitoring of colonies**

From 2000 to 2014, a total of 94 *R. hipposideros* maternity colonies were monitored in Brittany (Fig. 1). Not every colony was known in 2000, and, in some cases, monitoring was not possible due to unforeseen circumstances (blocked access to the bats or the person in charge of counting the bats). Thus, the number of monitored years per colony ranged from 3 to 14 (7.73 on average). This monitoring consisted of one or two counts during late June or early July, that is, during the period when newborns are easily distinguished from adults in Brittany. When multiple counts were carried out in a given year, only the largest one was considered. Adults and juveniles were counted separately: for each year, the census size of the colony was estimated by the number of adults, and the fecundity by the number of juveniles divided by the number of adults.

Colony size distribution is expected to correspond to a Poisson or a negative binomial distribution (O'Hara and Kotze 2010). Some colonies disappeared over the years, probably for reasons unrelated to the climatic variables considered: thus, we also considered zero-inflated Poisson and zero-inflated negative binomial distributions (Zuur et al. 2009). We tested which of these four distributions corresponded to our demographic data by using the



maximum likelihood method implemented in the R package *fitdistrplus* (Delignette-Muller and Dutang 2014). Fecundity was considered to follow a normal distribution. Generalized linear (count data) and linear (fecundity) mixed models together with Wald chi-square tests were used to test whether bat counts and fecundity varied between years. Colonies were considered as a random factor in the models, so as to not consider the impact of roost quality and environment. We then removed the random effects to plot the deviance residuals against the theoretical quantiles (QQ-plots) to check the assumptions of our models and detect possible outliers in the colonies. These tests, as well as the analyses described below, were carried out in R version 3.2.2 (R Development Core Team 2015).

## **Climatic data**

Minimum temperature, mean temperature, and precipitation were recorded monthly at 16 meteorological stations in Brittany (Météo-France data, <https://publitheque.meteo.fr>) since the beginning of the monitoring. Temperature directly influences the bats energy budget and their cost for homeothermy, but the most significant impact of temperature may also come from a decrease under particular thresholds: temperature low enough can induce torpor in bats or inhibit the flight of insects, needed for most bats foraging. Thus, both mean and minimum temperature have been considered in studies interested in the effect of climatic variables on bats (Reiter 2004a; Burles et al. 2009; López-Roig and Serra-Cobo 2014; Kerbiriou et al. 2015), and we decided to consider both of them here. Temperature and especially precipitation exhibited a great variability during the counting period (Fig. S1). We performed an ordinary kriging to obtain these climatic data for each colony by using the package "gstats", function "krige" (Pebesma 2004). Brittany's weather is spatially and temporally variable. We therefore performed a local kriging by taking into account only the three closest stations. Climatic information for each counting was then treated in three different ways. Firstly, each month of the previous life cycle (from August to July) was considered. These

data are thereafter named "monthly data". Secondly, we averaged the climatic information over longer periods corresponding to the mating period (September-November), hibernation (December-February), the spring transition (March-May) and parturition (June-July) periods. From now on, this temporal resolution is called "life cycle data". Thirdly, we averaged climatic data over the previous year, and refer to this temporal resolution as the "yearly data". Finally, we considered 17 of the 19 bioclimatic variables (Table 3) by computing our dataset the same way as ANUCLIM (Xu and Hutchinson 2013) with the help of the R package *climates* (Van der Wal et al. 2014) and refer to these as BIOCLIM data. The variable *bio7* correspond to *bio5* minus *bio6*, and caused linear combinations in our dataset: we thus excluded *bio7*, which is less informative than the two other variables, to avoid rank-deficiency in our models. The variables *bio 2* and *bio3* caused multiple correlations when in the same

model ( 
$$bio3 = \frac{bio2}{bio5 - bio6}$$
 ), and we discarded the less informative one, *bio3*.

Explanatory variables were centred and scaled prior to model fitting.

## Model averaging

Model averaging was performed to estimate the effect of climatic variables on colony size and fecundity. We created models explaining the variation in colony size (GLMM) and fecundity (LMM) depending on the climatic variables, by considering the different temporal resolutions. For monthly and life cycle data, models were computed separately for average temperatures, minimum temperatures, and precipitation. Two bioclimatic models were built considering separately temperature (BIOCLIM 1-11) and precipitation variables (BIOCLIM 12-19) to ease comparison with other models. Colonies were considered as a random factor in the models, and there were no temporal autocorrelations in those models (as explored using models residuals via the "acf" R function). Correlations between fixed effects were checked. Only *bio4* and *bio11* as well as *bio13* and *bio15* were highly correlated ( $r > 0.8$ ).

Full models were then used as bases in the glmulti R package to obtain every possible combination of explanatory variables (without interaction) and order them by AIC (Calcagno et al. 2010). Models including highly correlated variables ( $r > 0.8$ ) were discarded, and the package glmulti was then used to perform model averaging by calculating the Akaike weight of each model within  $2\Delta AIC$  of the best model (Burnham and Anderson 2002). The model-averaged regression coefficients of the predictors and their 95% confidence intervals (CI) were then calculated based on the cumulative weights of the models including the variable (Calcagno et al. 2010). Explanatory variables were then considered as having a meaningful positive or negative impact on the response variable if their 95% confidence interval did not include zero (Lankinen et al. 2016). The significance of yearly models, containing only one fixed effect (mean temperature, minimum temperature, or precipitation) and one random effect (colonies) were tested with Wald chi-square tests.

Model averaging with all temperature and precipitation monthly variables considered together would require very high computing power and memory (more than 16 million models to be evaluated and compared), especially for the colony size data and its more elaborate distributions. Thus, we created the mixed models that incorporated only significant predictors from previous model averaging (with either the minimum or average temperature, depending of the AIC) and computed their AIC and  $R^2$  (marginal and conditional - Nakagawa and Schielzeth 2013) to determine which kind of predictor and which temporal resolution best explained variations in colony size and fecundity of *R. hipposideros* colonies in Brittany. AIC was chosen over other criteria such as BIC because it is more appropriate for an exploratory analysis investigating which predictors could give the best description of a very complex system, whereas BIC is more performant in confirmatory analysis or hypothesis testing (Aho et al. 2014).

## Results

## **Variation of colony size and fecundity over the years**

Colony size data had a better fit with the zero-inflated negative binomial distribution (AIC : 6323.29), followed by the negative binomial, the zero-inflated Poisson and the Poisson distribution (with AIC of 6326.31, 21167.65 and 22596.92, respectively). Thus, we performed GLMMs with the zero-inflated negative binomial distribution. Both colony size and fecundity varied over the years (Wald chi-square test;  $p = 0.002$  and  $p < 0.001$  respectively).

## **Impact of climate**

Significant predictors were found for most monthly and life cycle models for both colony size (Table 1) and fecundity (Table 2). Annual climatic factors were never significant (Wald chi-square test;  $p > 0.15$  in all cases).

Comparisons of predictor categories and time resolutions showed that the models with the lowest AIC were those including monthly significant predictors for both colony size and fecundity. Precipitation model was the best for colony size, whereas the minimum temperature model had a lower AIC for fecundity

Colony size was positively influenced by precipitation in June and negatively impacted by October precipitation. Fecundity was positively impacted by the rain of October and negatively by precipitation during April. Monthly minimum temperature models had higher AIC than the corresponding monthly averaged temperature models for colony size, but lower in the case of fecundity. Nonetheless, they showed similar results regarding significant explanatory variables. Colony size was positively impacted by the temperature in May and November. Fecundity was positively influenced by the temperature during the months of April and July.

The AIC of the life cycle models were always larger than the corresponding monthly models ( $> 7 \Delta AIC$ ). Model averaging on life cycle data was not able to give any significant predictor when considering the impact of average or minimum temperature on colony size. Only precipitation during parturition time was found to be significant for colony size at the life cycle temporal scale. When looking at fecundity, the minimum temperature during spring transition and precipitation during mating period were significant. Yearly models were the models with the highest AIC (Table 1 and 2), and did not outperform the null model in most cases (AIC : 5755.42 and -37.15 for the null model of respectively the colony size and the fecundity dataset.)

There was no significant BIOCLIM predictor for colony size, but four variables were significant for fecundity (Table 3). Two factors positively affected fecundity: minimum temperature of the coldest month and precipitation of the wettest quarter. Annual precipitation and precipitation seasonality negatively impacted fecundity. The AIC of models built with these significant predictors were higher than those of monthly and life-cycle models.

Models with significant temperature (minimum for fecundity and average for colony size) and precipitation predictors were computed for each temporal resolution, as well as a model containing every bioclimatic predictor which was significant for both colony size and fecundity. Once again, the models with the lowest AIC were the monthly models, and the models with the highest AIC were yearly models, whilst those with life cycle and bioclimatic models were intermediate. Marginal  $R^2$  (Nakagawa and Schielzeth 2013) showed that the fixed effect of monthly models explained 0.9% and 5.3% of variability for colony size and fecundity, respectively, and ranking of marginal  $R^2$  was congruent with the AIC ranking (Table 4).

## Discussion

Colony size and fecundity varied between years and between colonies. Exploring whether these variations could be explained by climatic factors, we showed that fine temporal resolution climatic models have superior explanatory power compared to temporally coarse ones. These models reveal that climatic variables impact *R. hipposideros* population dynamics at critical periods, with more precipitation having significant and opposite impacts depending on the time of year, and increased temperatures having a positive impact.

### **Temporal resolution of weather impact**

Life cycle data correspond to meteorological data averaged over specific periods built upon the biology and life cycle of species. These averages are commonly used in studies interested in exploring climatic impacts on species demographic dynamics. For *R. hipposideros*, the periods were chosen according to bibliography and expert knowledge. Using AIC selection, we showed that abiotic factors calculated with monthly resolution better predicted the *R. hipposideros* colony size and fecundity in Brittany compared to the factors calculated with coarser resolution. These results can be explained by the great climate variability observed between months, especially for precipitation (Fig. S1). Our results also suggest that the same variable can have either positive or negative effects depending on the period of the year. This implies that in regions like Brittany, population dynamic processes are mainly dependent on critical periods which are shorter than life cycle periods. Those critical periods are supposedly highly dependent on the interaction between the species biology and the local climate.

One could argue that comparisons of models using AIC tend to favour complex models (Link and Barker 2006). We however did not observe this when computing AIC for full models that included all variables (both non-significant and significant predictors, data not shown). The use of model averaging instead of other approaches such as stepwise AIC

also allowed us to only consider significant predictors and limits bias towards over-complex models (Lukacs et al. 2010). Besides providing estimates and confidence intervals, model averaging also measures the importance of each variable, based on the AIC of the models where they were included, the so called "sum of weight". The sum of weight of each significant predictor in our study was superior to 0.95 (data not shown), further supporting the importance of these variables in explaining variations in colony size and fecundity in the lesser horseshoe bat (Giam and Olden 2016).

Considering all the models which are at 2  $\Delta$ AIC from the best model is a common practice in model averaging, but it has been argued that even models below this threshold should be included in the analysis, and that being too stringent could exclude significant variables (Burnham et al. 2011). In the case of our results, monthly data gave still better predictors than life cycle data when we extended the threshold until 7  $\Delta$ AIC. However, it caused the disappearance of some significant variables instead of the appearance of new ones (see supplementary materials, Tables S1 and S2). Multicollinearity in the averaged models was suspected, but excluding all the models with Variance Inflation Factors higher than 2 did not change the results (data not shown). The disappearance of significant variables can be due to the fact that we considered every month or period of the year without any a priori, and thus probably included some non-relevant variables. Increasing the threshold to 7  $\Delta$ AIC led to the inclusion of poor models, which are known to impact the results and increase confidence intervals around effect sizes (Burnham and Anderson 2002). Indeed, models including significant predictors obtained with 2  $\Delta$ AIC had lower AIC than models including significant predictors obtained with 7  $\Delta$ AIC (compare Tables 1 to S1 and 2 to S2). Thus, we only considered the 2  $\Delta$ AIC results in the following discussion.

Depending on climate variability, averaging weather variables over long periods could result in the concealment or misidentification of essential impacts on population dynamics.

Comparisons between climate variables averaged yearly or over shorter periods already showed that short-term climatic conditions are better at characterising population dynamics (Gedir et al. 2015). This was also shown in mechanistic models, which in contrast with our correlative approach directly model the relationship between individual traits and the environment. Those models generally use finer temporal scale resolution than correlative models, and it has been shown that reducing the environmental data to a daily resolution permitted a better understanding of environmental impact (Kearney et al. 2012). Our results suggest that even periods of several-months which are consistent with the life cycle of the species, and which are commonly used in explanatory correlative studies, could be too long to really grasp the effect of climate on species. Likewise, the now widely used BIOCLIM variables (Barbet-Massin and Jetz 2014; Del Toro et al. 2015; Beltramino et al. 2015; Ray et al. 2016) were far less predictive than monthly variables, and did not result in better models than our life cycle variables. Interestingly though, BIOCLIM variables included variables that were not present in the other models, such as precipitation seasonality that appeared to significantly explain fecundity.

Studies interested in the impact of climate on demographic parameters would therefore greatly benefit from considering explanatory variables with fine temporal resolution (e.g. monthly). One could argue that considering a short temporal resolution implies multiplying the number of variables used in those models. One solution could be to only consider a few months based on the species biology (Kerbiriou et al. 2015), but the best way might be to select the most relevant predictors by statistical means before performing other analyses (Parent et al. 2016; van de Pol et al. 2016). To this end, model averaging is an ideal tool for selecting significant predictors. A recently released R package, *climwin*, is also a well-designed tool to address the question of temporal resolution. Though it allows a great flexibility to easily detect the best time window based on AIC comparisons, it is not well-



optimized for detecting multiple effect of the same variable (van de Pol et al. 2016). Our example demonstrates that situations may include multiple effects of the same variable, and we advocate the use of alternative and complementary tools to understand how species respond to environmental variation, which is one of the main challenges when the aim is to predict the future of biodiversity (Urban et al. 2016).

Indeed, temporal resolution is also an important feature when predicting the impact of future climate change on species distribution, a topic which has received increasing interest in the scientific community. If global or regional climate change are generally considered on a yearly (or coarser temporal) basis when it comes to prediction (Turner et al. 1989), coarse temporal resolution will fail to grasp the heterogeneity of responses and could substantially alter the outcome of population viability predictions under temperature change scenarios (Radchuk et al. 2014). Reducing the temporal resolution for species distribution models is particularly important when dealing with microclimate (Kearney and Porter 2009). The future species distribution of European bats, including *R. hipposideros*, has been predicted in a recent study based on climate variables averaged over 30 years (Rebelo et al. 2010). This pooling is understandable given the number of species, and the prediction time span (2050 and 2090), but the impact of temporal resolution on these models has not been, to our knowledge, deeply investigated. Despite the fact that the processes considered in this study are not directly related to range distribution, it would be interesting to test different temporal resolutions when conducting distribution modelling for species that experience highly variable climatic conditions like *R. hipposideros*.

### **Impact of weather on *R. hipposideros***

*R. hipposideros* colony size and fecundity significantly varied between years. Variances explained by the fixed effect of our models were low, especially for the colony size models,

but the variance explained by the fecundity model was within the range of variance usually explained by most ecology models (Møller and Jennions 2002). In a study on a pipistrelle bat population, Kerbiriou et al. (2015) have shown that the variance of meaningful environmental variables (including climatic variables) could be drastically reduced (to 1%) because of intrinsic demographic trends. Additionally, although *R. hipposideros* is a rather sedentary species (Dool et al. 2016), we do not consider emigration or immigration which could influence the colony size besides the effect of climate. Thermal isolation of the roosts/hibernacula could also modify the impact of the ambient temperature during summer or winter. Even though we cannot predict which part of the environmental variance those variables explain (Sæther et al. 2000), our results nevertheless pinpoint mechanisms by which climatic factors play a role in the inter-annual variation of colony size and fecundity of *R. hipposideros*.

Precipitation was the climatic factor that best explained the variation in colony size. Rainfall directly impacts bats by increasing the energetic cost of flight and homeothermy and by making echolocation less efficient, but also indirectly by acting on insect abundance and hence on food availability (Grindal et al. 1992; Frick et al. 2010; Voigt et al. 2011). If a greater effect of the precipitation on bats compared to temperature has been observed in warmer climates (Hoyle et al. 2001; Frick et al. 2012), this was unexpected for European insectivorous bats (Rebelo et al. 2010). This could be explained by the greater variability of precipitation in Brittany (Fig. S1) that would have increased the support for this variable in our models (Frick et al. 2010).

An interesting result is that depending on the month and the demographic variable considered, precipitation had a positive or a negative impact. If the ambiguous impact of rain on bats, depending on region and time, has already been reported (Frick et al. 2010; Lučan et al. 2013), this study is to our knowledge, the first where precipitation is shown to have

significant and opposite impacts on the same bat population depending on the time of the year. The impact of precipitation on the colony size was negative in October but positive in June. Precipitation impact on bat population dynamics differs depending on the timing of precipitation (Frick et al. 2010), either negatively by increasing the energy cost for foraging (Voigt et al. 2011) and decreasing the efficiency of echolocation (Griffin 1971), or positively by increasing insect abundance in dryer periods (Williams 1951). Opposite effects of the same factor, caused by spatial or temporal variability, has already been observed in a wide range of species (Spiller and Schoener 2008; Satterthwaite et al. 2012; Metz and Tielboerger 2016), but these results highlight the necessity to have the finest temporal resolution possible to enhance our understanding of the impact of climatic factors. Thus, it seems that precipitation impact can be highly variable in Brittany, with an overall negative effect except during summer, which is the driest period. The positive impact of rain during October on fecundity is more surprising given that it has the opposite effect on colony size. Opposite climate or environmental effects on survival and fecundity have already been observed in other species such as emperor penguins (Barbraud and Weimerskirch 2001), Eurasian oystercatchers (Van de Pol et al. 2010) or goshawks (Herfindal et al. 2015). Those results signal a complex pattern of co-variation that would need further investigation and a better understanding of the underlying mechanisms.

Low temperatures can influence bat survival by directly increasing energetic cost for homeothermy, but also by reducing insect activity and so food availability (Reiter 2004a; Burles et al. 2009). The colony size in *R. hipposideros* was positively impacted by higher temperatures during the period when individuals return to their maternity roosts and hibernacula (May and November, respectively). We can thus hypothesize that the temperature of these months would strongly impact the bats' energy budget for parturition and hibernation.

Because the flight of most insects is inhibited under some threshold temperature (Taylor 1963), it is more impacted by minimum than average temperatures . A stronger influence of the minimum temperature than of average temperature on fecundity of *R. hipposideros* suggests that this process depends on food availability at some critical periods. April seems to be the key month regarding fecundity. Inclement weather, e.g. cold and rainy, during the early foetal stage, is known to cause abortion or resorption of embryos in bats (Grindal et al. 1992; Lučan et al. 2013) which could explain the observed negative impact of precipitation and the positive impact of minimum temperature in April on fecundity. The impact of temperature during July, the lactating period in Brittany, is also not surprising, because a cold month is expected to reduce the survival rate of juveniles, diminishing reproductive success (Reiter 2004a; Burles et al. 2009).

Results based on BIOCLIM variables gave a consistent pattern, with notably a positive impact of the higher minimum temperature and a negative impact of precipitation except for the wettest quarter (which would correspond approximately to autumn in Brittany). Even if the AIC of BIOCLIM models were higher than monthly models, there are two significant variables that could not be detected by our other models, which are temperature and precipitation seasonality, with a positive and negative impact respectively. Adding those variables to monthly models did not change the significant predictors (data not shown), but the impact of climate seasonality on bat fecundity deserves further investigation.

## **Conclusion**

Considering the temporal resolution of weather variables allowed the detection of climate impact on a bat population of high conservation priority at a very fine resolution. Relaxing the assumption that the impact of weather variables is invariant during life cycle periods was here important to uncover the effects of climate on colony sizes and fecundity in

463 the lesser horseshoe bat. Because most climate databases offer at least a monthly resolution,  
464 we suggest that analogous studies should consider fine temporal resolution for testing the  
465 impact of continuous abiotic variables such as those linked to weather. Although our approach  
466 was correlative, it enabled the identification of potential mechanisms by which climatic  
467 factors affect population dynamics. Obtaining this knowledge is a necessary step towards  
468 better forecasts of biodiversity responses under climate change.

469

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713 **Data Accessibility:**

714 Data used in this study were deposited at DRYAD entry XXXXXXXX

715 **Table 1:** Colony size as a function of average temperature, minimum temperature and precipitation at different temporal resolutions. Monthly  
716 models consider each month from August to July preceding bat counts. Life cycle models consider mating, hibernation, spring transition and  
717 parturition period (August month was excluded). Yearly models only consider the climatic variable averaged over the year. NS : non-significant  
718 predictor after model averaging (monthly and life cycle models) or non-significant Wald chi-square test (yearly models); + : positive significant  
719 predictor; - : negative significant predictor. Model averaging was based on AIC (see text). Last rows display the AIC of the models only  
720 containing the significant predictors as fixed effects, and finally their corresponding rank.

		Monthly models			Life cycle models			Yearly models		
		Aver. Temp.	Min. Temp.	Precip.	Aver. Temp.	Min. Temp.	Precip.	Aver. Temp.	Min. Temp.	Precip.
Mating	August	NS	NS	NS						
	September	NS	NS	NS						
	October	NS	NS	-	NS	NS	NS			
	November	+	+	NS						
Hibernation	December	NS	NS	NS						
	January	NS	NS	NS	NS	NS	NS	NS	NS	NS
	February	NS	NS	NS						
Spring Transition	March	NS	NS	NS						
	April	NS	NS	NS	NS	NS	NS			
	May	+	+	NS						
Parturition	June	NS	NS	+	NS	NS	+			
	July	NS	NS	NS						
AIC - Significant predictor		5748.96	5749.26	<b>5743.98</b>	NA	NA	5751.2	5757.36	5757.42	5757.36
(Rank)		(2)	(3)	(1)			(3)	(5)	(6)	(5)

**Table 2:** Fecundity as a function of average temperature, minimum temperature and precipitation at different temporal resolutions. Legend and format are identical to those of Table 1.

		Monthly models			Life cycle models			Yearly models					
		Aver. Temp.	Min. Temp.	Precip.	Aver. Temp.	Min. Temp.	Precip.	Aver. Temp.	Min. Temp.	Precip.			
Mating	August	NS	NS	NS				NS	NS	NS			
	September	NS	NS	NS	NS	NS	+						
	October	NS	NS	+									
	November	NS	NS	NS									
Hibernation	December	NS	NS	NS	NS	NS	NS				NS	NS	NS
	January	NS	NS	NS									
	February	NS	NS	NS									
Spring Transition	March	NS	NS	NS	NS	+	NS				NS	NS	NS
	April	+	+	-									
	May	NS	NS	NS									
Parturition	June	NS	NS	NS	NS	NS	NS				NS	NS	NS
	July	+	+	NS									
AIC - Significant predictor		-55.24	-61.35	-57.55	NA	-42.24	-47.25	-35.60	-38.34	-35.79			
(Rank)		(3)	(1)	(2)		(5)	(4)	(8)	(6)	(7)			

729 **Table 3:** Impact of temperature and precipitation BIOCLIM variables on *Rhinolophus hipposideros* fecundity. Model averaging was performed  
730 on two models separating temperature and precipitation variables. BIOCLIM variables 3 and 7 were excluded from our analysis (see text). NS:  
731 non-significant predictor after model averaging; +: positive significant predictor; -: negative significant predictor. Last columns display the AIC  
732 of the models only containing the significant predictors as fixed effects.

	Variable Description	Number (BIOCLIM)	Significance	Significant predictors
Temperature	Annual mean temperature	1	NS	-37.78
	Mean diurnal range	2	NS	
	Isothermality (2/7)	3		
	Temperature seasonality	4	NS	
	Maximum temperature of warmest month	5	NS	
	Minimum temperature of coldest month	6	+	
	Temperature annual range (5-6)	7		
	Mean temperature of wettest quarter	8	NS	
	Mean temperature of driest quarter	9	NS	
	Mean temperature of the warmest quarter	10	NS	
	Mean temperature of coldest quarter	11	NS	
Precipitation	Annual precipitation	12	-	-43.30
	Precipitation of wettest month	13	NS	
	Precipitation of driest month	14	NS	
	Precipitation seasonality	15	-	
	Precipitation of wettest quarter	16	+	
	Precipitation of driest quarter	17	NS	
	Precipitation of the warmest quarter	18	NS	
	Precipitation of the coldest quarter	19	NS	

733 **Table 4:** AIC and ranks of models that included both minimum temperature and precipitation significant predictors for the different temporal  
734 resolutions of explanatory variables.

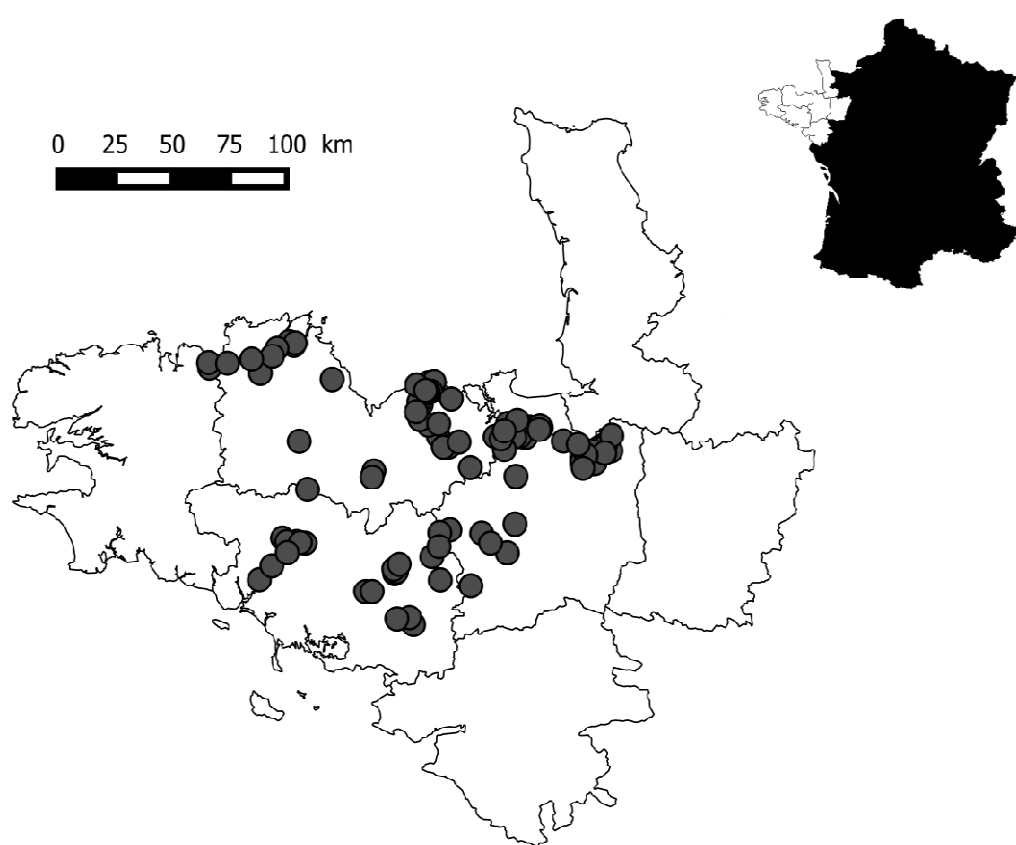
Fixed effects		AIC (Rank)	Marginal R <sup>2</sup>	Conditional R <sup>2</sup>	
Census size	Month	Minimum temperature : November & May Precipitation : October & June	5746.74 (1)	0.009	0.669
	Life cycle	Precipitation : Parturition	5751.2 (2)	0.003	0.658
	Year	Minimum temperature : Year Precipitation : Year	5759.3 (3)	<0.001	0.654
	BIOCLIM	NA	NA	NA	NA
Fecundity	Month	Minimum temperature : April & July Precipitation : October & April	-65.14 (1)	0.053	0.177
	Life cycle	Minimum temperature : Spring Transition Precipitation : Mating	-51.79 (2)	0.027	0.154
	Year	Minimum temperature : Year Precipitation : Year	-36.48 (4)	0.006	0.123
	BIOCLIM	Temperature : 6 Precipitation : 12,15 & 16	-43.72 (3)	0.021	0.148

735 **Figure legends**

736 **Figure 1:** Map of the 94 colonies monitored in Brittany, France.

737

738 **Figure 1**



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