

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

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

20 *Determining the temporal resolution of climatic variables when identifying their impact on*  
21 *wild population abundance is a rising concern. Our work proposes a way free of most*  
22 *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.

23 **Abstract**

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

42 **Key Words**

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

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## 48 **Introduction**

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

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

97           Studies of bat population dynamics usually take into account weather as one of the  
98 fundamental explanatory variables. Those studies are mainly based on counts or captures  
99 made at one particular moment in the life cycle, such as during parturition or the hibernation  
100 period (Grindal et al. 1992; Zahn 1999; Hoyle et al. 2001; López-Roig and Serra-Cobo 2014;  
101 Kerbiriou et al. 2015). Climatic factors usually include rainfall and temperature, which can be  
102 the daily mean (Zahn 1999; Schorcht et al. 2009; Kerbiriou et al. 2015) or minimum  
103 temperature (Grindal et al. 1992; Hoyle et al. 2001; López-Roig and Serra-Cobo 2014). Some  
104 other variables, such as drought severity, winter severity or winter duration, can also be  
105 included, using different proxies (Schorcht et al. 2009; López-Roig and Serra-Cobo 2014;  
106 Amorim et al. 2015; Kerbiriou et al. 2015). Once again, the time resolution of these variables  
107 differs between studies, and climatic factors can be considered for specific months (Grindal et  
108 al. 1992; Zahn 1999; Kerbiriou et al. 2015), averaged over seasons consistent with the species  
109 biology (Schorcht et al. 2009; Frick et al. 2010; Adams 2010; López-Roig and Serra-Cobo  
110 2014), or averaged over even longer periods (Hoyle et al. 2001; Amorim et al. 2015).

111           The lesser horseshoe bat (*Rhinolophus hipposideros*) is a small insectivorous bat of  
112 recognized conservation concern (Bontadina et al. 2000). This bat forages exclusively in  
113 woodlands, preferentially in dense areas (Bontadina et al. 2002; Reiter 2004b), and is already  
114 considered as a good indicator of biodiversity loss (Haysom et al. 2013). After the last  
115 glaciation, this species expanded its range from southern Europe to northern parts of Europe  
116 (Dool et al. 2013), into environments with colder and less stable climate (Bontadina et al.  
117 2000). In spring, females leave the underground sites used as hibernacula and gather in  
118 maternity roosts, which are generally in warmer places, like attics, and the parturition and  
119 rearing of offspring takes place during June and July. Mating then occurs principally between  
120 the end of September and the beginning of the hibernation period (Gaisler 1966). The life  
121 cycle and activity of *R. hipposideros* are particularly affected by weather conditions. This bat

122 prefers higher temperature for its maternity roost than other attic dwelling species  
123 (Kayikcioglu and Zahn 2004). However, if available, they will switch to colder satellite roosts  
124 if temperatures become too high during summer. These observations suggest direct effects of  
125 weather on the thermoregulation and energy budget (Kayikcioglu and Zahn 2004;  
126 Seckerdieck et al. 2005). Inclement weather (i.e. cool and wet) before parturition generally  
127 delays birth and decreases the average size at birth and growth rate of the juveniles. These  
128 effects are explained by energetic costs, implying more torpor and a slowed metabolism for  
129 pregnant females, as well as by decreased food availability (Reiter 2004a). However, the  
130 global effect of weather conditions on the overall population dynamics of *R. hipposideros*,  
131 crucial information for understanding population trends, is not documented (Bontadina et al.  
132 2000).

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

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

## 154 **Material and Methods**

### 155 **Monitoring of colonies**

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

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



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

## 180 **Climatic data**

181 Minimum temperature, mean temperature, and precipitation were recorded monthly at  
182 16 meteorological stations in Brittany (Météo-France data, <https://publitheque.meteo.fr>) since  
183 the beginning of the monitoring. Temperature directly influences the bats energy budget and  
184 their cost for homeothermy, but the most significant impact of temperature may also come  
185 from a decrease under particular thresholds: temperature low enough can induce torpor in bats  
186 or inhibit the flight of insects, needed for most bats foraging. Thus, both mean and minimum  
187 temperature have been considered in studies interested in the effect of climatic variables on  
188 bats (Reiter 2004a; Burles et al. 2009; López-Roig and Serra-Cobo 2014; Kerbiriou et al.  
189 2015), and we decided to consider both of them here. Temperature and especially  
190 precipitation exhibited a great variability during the counting period (Fig. S1). We performed  
191 an ordinary kriging to obtain these climatic data for each colony by using the package  
192 "gstats", function "krige" (Pebesma 2004). Brittany's weather is spatially and temporally  
193 variable. We therefore performed a local kriging by taking into account only the three closest  
194 stations. Climatic information for each counting was then treated in three different ways.  
195 Firstly, each month of the previous life cycle (from August to July) was considered. These

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

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

208 Explanatory variables were centred and scaled prior to model fitting.

### 209 **Model averaging**

210 Model averaging was performed to estimate the effect of climatic variables on colony  
211 size and fecundity. We created models explaining the variation in colony size (GLMM) and  
212 fecundity (LMM) depending on the climatic variables, by considering the different temporal  
213 resolutions. For monthly and life cycle data, models were computed separately for average  
214 temperatures, minimum temperatures, and precipitation. Two bioclimatic models were built  
215 considering separately temperature (BIOCLIM 1-11) and precipitation variables (BIOCLIM  
216 12-19) to ease comparison with other models. Colonies were considered as a random factor in  
217 the models, and there were no temporal autocorrelations in those models (as explored using  
218 models residuals via the "acf" R function). Correlations between fixed effects were checked.  
219 Only bio4 and bio11 as well as bio13 and bio15 were highly correlated ( $r > 0.8$ ).

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

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

## 244 **Results**

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

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

## 251 **Impact of climate**

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

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

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

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

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

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

290   **Discussion**

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

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

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

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

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

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

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

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

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



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

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

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

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

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

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

410 An interesting result is that depending on the month and the demographic variable considered,  
411 precipitation had a positive or a negative impact. If the ambiguous impact of rain on bats,  
412 depending on region and time, has already been reported (Frick et al. 2010; Lučan et al.  
413 2013), this study is to our knowledge, the first where precipitation is shown to have

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

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

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

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

## 458 **Conclusion**

459           Considering the temporal resolution of weather variables allowed the detection of  
460 climate impact on a bat population of high conservation priority at a very fine resolution.  
461 Relaxing the assumption that the impact of weather variables is invariant during life cycle  
462 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)

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

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		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	+			
	November	NS	NS	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			
	May	NS	NS	NS						
Parturition	June	NS	NS	NS	NS	NS	NS			
	July	+	+	NS						
AIC - Significant predictor		-55.24	<b>-61.35</b>	-57.55	NA	-42.24	-47.25	-35.60	-38.34	-35.79
(Rank)		(3)	(1)	(2)		(5)	(4)	(8)	(6)	(7)

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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	
	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	+	-37.78
	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	-	
	Precipitation of wettest month	13	NS	
	Precipitation of driest month	14	NS	
	Precipitation seasonality	15	-	
	Precipitation of wettest quarter	16	+	-43.30
	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.

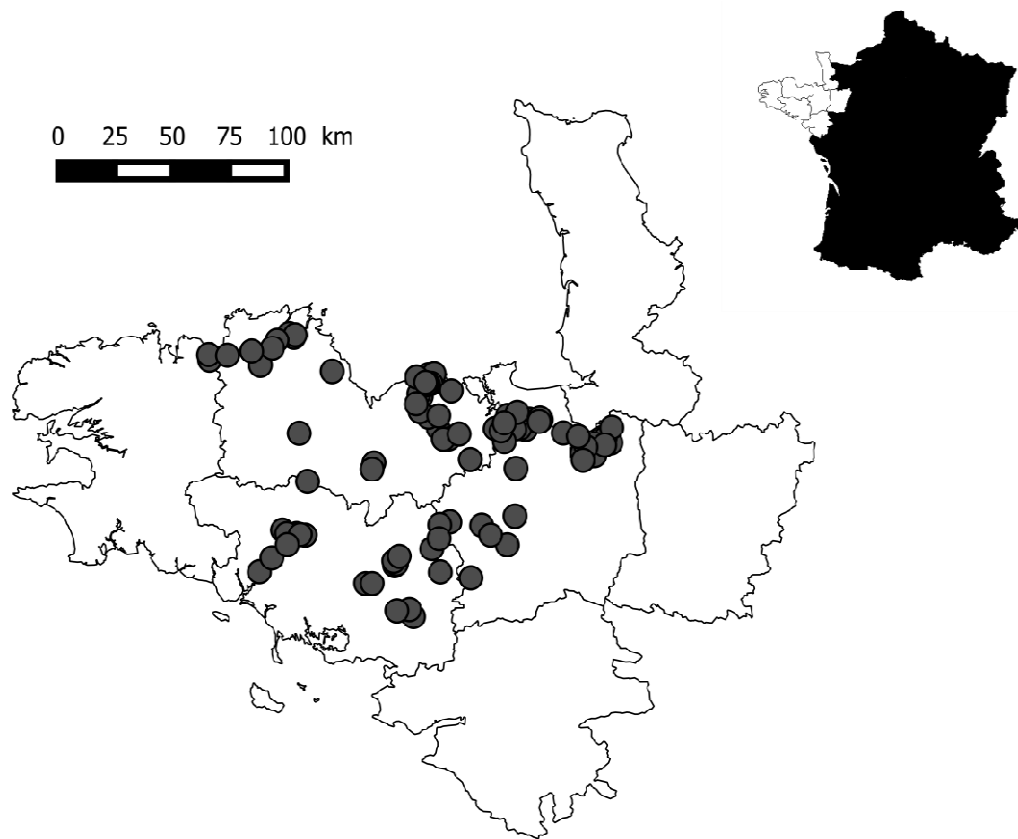
	Fixed effects	AIC (Rank)	Marginal R <sup>2</sup>	Conditional R <sup>2</sup>
Census size	Month Minimum temperature : November & May Precipitation : October & June	5746.74 (1)	0.009	0.669
	Life cycle Precipitation : Parturition	5751.2 (2)	0.003	0.658
	Year Minimum temperature : Year Precipitation : Year	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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