

# 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
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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

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

42 Key Words

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

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#### 48 Introduction

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

In this context, understanding the impact of climatic factors on population dynamics 58 and demography appears to be fundamental to interpret or predict long term population trends 59 (McLean et al. 2016; Urban et al. 2016). This topic has been studied for many species, 60 61 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 62 then modelled as a function of weather, considering mainly temperature and rainfall, but 63 sometimes including other variables (Bruggeman et al. 2015; Kerbiriou et al. 2015; Bleho et 64 al. 2015; Kanno et al. 2016; Dugger et al. 2016). Obviously, variables included in the model 65 directly depend on the considered species biology, but more surprisingly, the temporal 66 resolution considered is also highly variable. The latter citations correspond to recent studies 67 that deal with various taxa, and all of them have used climatic databases offering a monthly (if 68 69 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 70 preliminary analysis (Parent et al. 2016) or on expert knowledge (Kerbiriou et al. 2015). Most 71 72 studies have aggregated climatic data to correspond to climatic seasons (varying from two to

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

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

Studies of bat population dynamics usually take into account weather as one of the 97 98 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 99 100 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 101 the daily mean (Zahn 1999; Schorcht et al. 2009; Kerbiriou et al. 2015) or minimum 102 temperature (Grindal et al. 1992; Hoyle et al. 2001; López-Roig and Serra-Cobo 2014). Some 103 104 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; 105 106 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 107 al. 1992; Zahn 1999; Kerbiriou et al. 2015), averaged over seasons consistent with the species 108 109 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). 110

The lesser horseshoe bat (*Rhinolophus hipposideros*) is a small insectivorous bat of 111 recognized conservation concern (Bontadina et al. 2000). This bat forages exclusively in 112 woodlands, preferentially in dense areas (Bontadina et al. 2002; Reiter 2004b), and is already 113 considered as a good indicator of biodiversity loss (Haysom et al. 2013). After the last 114 115 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. 116 2000). In spring, females leave the underground sites used as hibernacula and gather in 117 118 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 119 the end of September and the beginning of the hibernation period (Gaisler 1966). The life 120 121 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 122 123 (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 124 125 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 126 delays birth and decreases the average size at birth and growth rate of the juveniles. These 127 effects are explained by energetic costs, implying more torpor and a slowed metabolism for 128 129 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*, 130 131 crucial information for understanding population trends, is not documented (Bontadina et al. 2000). 132

As climatic impact can greatly differ depending on the level of response considered 133 (McLean et al. 2016), we investigated two proxies of the dynamics of R. hipposideros 134 135 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 136 on these parameters, we used count data from 94 colonies (Brittany, France) collected by 137 local associations during fifteen years. These count data offer reliable estimates of colony size 138 as confirmed by independent non-invasive Capture-Mark Recapture methods (Puechmaille 139 140 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 141 influenced by the weather (Thomas et al. 1994; Geber 2008; Bateman et al. 2011). 142 143 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 144 Dubreuil 2010). Our study had two objectives: 1) investigating the temporal resolution at 145 146 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.

#### 154 Material and Methods

#### 155 Monitoring of colonies

From 2000 to 2014, a total of 94 R. hipposideros maternity colonies were monitored in 156 Brittany (Fig. 1). Not every colony was known in 2000, and, in some cases, monitoring was 157 not possible due to unforeseen circumstances (blocked access to the bats or the person in 158 159 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 160 early July, that is, during the period when newborns are easily distinguished from adults in 161 162 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 163 colony was estimated by the number of adults, and the fecundity by the number of juveniles 164 divided by the number of adults. 165

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

maximum likelihood method implemented in the R package fitdistrplus (Delignette-Muller 171 172 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 173 174 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 175 and environment. We then removed the random effects to plot the deviance residuals against 176 the theoretical quantiles (QQ-plots) to check the assumptions of our models and detect 177 possible outliers in the colonies. These tests, as well as the analyses described below, were 178 carried out in R version 3.2.2 (R Development Core Team 2015). 179

#### 180 Climatic data

Minimum temperature, mean temperature, and precipitation were recorded monthly at 181 16 meteorological stations in Brittany (Météo-France data, https://publitheque.meteo.fr) since 182 183 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 184 from a decrease under particular thresholds: temperature low enough can induce torpor in bats 185 186 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 187 bats (Reiter 2004a; Burles et al. 2009; López-Roig and Serra-Cobo 2014; Kerbiriou et al. 188 189 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 190 191 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 192 variable. We therefore performed a local kriging by taking into account only the three closest 193 194 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 195

data are thereafter named "monthly data". Secondly, we averaged the climatic information 196 197 over longer periods corresponding to the mating period (September-November), hibernation (December-February), the spring transition (March-May) and parturition (June-July) periods. 198 199 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". 200 Finally, we considered 17 of the 19 bioclimatic variables (Table 3) by computing our dataset 201 the same way as ANUCLIM (Xu and Hutchinson 2013) with the help of the R package 202 203 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 204 excluded bio7, which is less informative than the two other variables, to avoid rank-deficiency 205 in our models. The variables bio 2 and bio3 caused multiple correlations when in the same 206

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

Model averaging was performed to estimate the effect of climatic variables on colony 210 211 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 212 resolutions. For monthly and life cycle data, models were computed separately for average 213 temperatures, minimum temperatures, and precipitation. Two bioclimatic models were built 214 215 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 216 217 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. 218 Only bio4 and bio11 as well as bio13 and bio15 were highly correlated (r>0.8). 219

Full models were then used as bases in the glmulti R package to obtain every possible 220 221 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 222 223 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-224 averaged regression coefficients of the predictors and their 95% confidence intervals (CI) 225 were then calculated based on the cumulative weights of the models including the variable 226 227 (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 228 229 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 230 effect (colonies) were tested with Wald chi-square tests. 231

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

#### 244 **Results**

#### 245 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).

#### 251 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).

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

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

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

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

Life cycle data correspond to meteorological data averaged over specific periods built 298 upon the biology and life cycle of species. These averages are commonly used in studies 299 interested in exploring climatic impacts on species demographic dynamics. For R. 300 *hipposideros*, the periods were chosen according to bibliography and expert knowledge. 301 302 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 303 calculated with coarser resolution. These results can be explained by the great climate 304 305 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 306 period of the year. This implies that in regions like Brittany, population dynamic processes 307 are mainly dependent on critical periods which are shorter than life cycle periods. Those 308 critical periods are supposedly highly dependent on the interaction between the species 309 310 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 322 practice in model averaging, but it has been argued that even models below this threshold 323 should be included in the analysis, and that being too stringent could exclude significant 324 325 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 326 caused the disappearance of some significant variables instead of the appearance of new ones 327 328 (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 329 not change the results (data not shown). The disappearance of significant variables can be due 330 to the fact that we considered every month or period of the year without any a priori, and thus 331 332 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 333 intervals around effect sizes (Burnham and Anderson 2002). Indeed, models including 334 significant predictors obtained with 2  $\Delta$ AIC had lower AIC than models including significant 335 336 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. 337

338 Depending on climate variability, averaging weather variables over long periods could339 result in the concealment or misidentification of essential impacts on population dynamics.

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

Studies interested in the impact of climate on demographic parameters would therefore 355 greatly benefit from considering explanatory variables with fine temporal resolution (e.g. 356 monthly). One could argue that considering a short temporal resolution implies multiplying 357 358 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 359 select the most relevant predictors by statistical means before performing other analyses 360 361 (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-362 designed tool to address the question of temporal resolution. Though it allows a great 363 364 flexibility to easily detect the best time window based on AIC comparisons, it is not welloptimized 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).

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

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

387 *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 389 390 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 391 variables (including climatic variables) could be drastically reduced (to 1%) because of 392 intrinsic demographic trends. Additionally, although R. hipposideros is a rather sedentary 393 species (Dool et al. 2016), we do not consider emigration or immigration which could 394 influence the colony size besides the effect of climate . Thermal isolation of the 395 roosts/hibernacula could also modify the impact of the ambient temperature during summer or 396 winter. Even though we cannot predict which part of the environmental variance those 397 398 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. 399 hipposideros. 400

Precipitation was the climatic factor that best explained the variation in colony size. 401 402 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 403 hence on food availability (Grindal et al. 1992; Frick et al. 2010; Voigt et al. 2011). If a 404 greater effect of the precipitation on bats compared to temperature has been observed in 405 warmer climates (Hoyle et al. 2001; Frick et al. 2012), this was unexpected for European 406 407 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 408 our models (Frick et al. 2010). 409

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 414 415 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 416 417 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 418 by increasing insect abundance in dryer periods (Williams 1951). Opposite effects of the same 419 factor, caused by spatial or temporal variability, has already been observed in a wide range of 420 species (Spiller and Schoener 2008; Satterthwaite et al. 2012; Metz and Tielboerger 2016), 421 but these results highlight the necessity to have the finest temporal resolution possible to 422 423 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 424 summer, which is the driest period. The positive impact of rain during October on fecundity is 425 426 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 de Pol et al. 2010) or goshawks (Herfindal et al. 2015). Those results signal a complex pattern 429 of co-variation that would need further investigation and a better understanding of the 430 431 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 439 440 (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. 441 442 *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, 443 during the early foetal stage, is known to cause abortion or resorption of embryos in bats 444 (Grindal et al. 1992; Lučan et al. 2013) which could explain the observed negative impact of 445 precipitation and the positive impact of minimum temperature in April on fecundity. The 446 impact of temperature during July, the lactating period in Brittany, is also not surprising, 447 because a cold month is expected to reduce the survival rate of juveniles, diminishing 448 reproductive success (Reiter 2004a; Burles et al. 2009). 449

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

#### 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

- 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.

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#### 470 **References**

- 471 Adams RA (2010) Bat reproduction declines when conditions mimic climate change
- 472 projections for western North America. Ecology 91:2437–2445.
- 473 Adams RA, Hayes MA (2008) Water availability and successful lactation by bats as related to
- 474 climate change in arid regions of western North America. J Anim Ecol 77:1115–1121. doi:
- 475 10.1111/j.1365-2656.2008.01447.x
- 476 Aho K, Derryberry D, Peterson T (2014) Model selection for ecologists: the worldviews of
- 477 AIC and BIC. Ecology 95:631–636.
- 478 Akesson S (2016) Flying with the winds: differential migration strategies in relation to winds
- 479 in moth and songbirds. J Anim Ecol 85:1–4. doi: 10.1111/1365-2656.12450
- 480 Amorim F, Rebelo H, Rodrigues L (2012) Factors influencing bat activity and mortality at a
- 481 wind farm in the mediterranean Region. Acta Chiropterol 14:439–457. doi:
- 482 10.3161/150811012X661756
- 483 Amorim F, Mata VA, Beja P, Rebelo H (2015) Effects of a drought episode on the
- 484 reproductive success of European free-tailed bats (*Tadarida teniotis*). Mamm Biol 80:228–
- 485 236. doi: 10.1016/j.mambio.2015.01.005
- 486 Barbet-Massin M, Jetz W (2014) A 40-year, continent-wide, multispecies assessment of
- relevant climate predictors for species distribution modelling. Divers Distrib 20:1285–1295.
- 488 doi: 10.1111/ddi.12229
- Barbraud C, Weimerskirch H (2001) Emperor penguins and climate change. Nature 411:183–
  186. doi: 10.1038/35075554

- 491 Bateman BL, Abell-Davis SE, Johnson CN (2011) Climate-driven variation in food
- 492 availability between the core and range edge of the endangered northern bettong (*Bettongia*
- 493 *tropica*). Aust J Zool 59:177–185. doi: 10.1071/ZO11079
- 494 Beltramino AA, Vogler RE, Gutiérrez Gregoric DE, Rumi A (2015) Impact of climate change
- 495 on the distribution of a giant land snail from South America: predicting future trends for
- 496 setting conservation priorities on native malacofauna. Clim Change 131:621–633. doi:
- 497 10.1007/s10584-015-1405-3
- 498 Bleho BI, Koper N, Borkowsky CL, Hamel CD (2015) Effects of weather and land
- 499 management on the western prairie fringed-orchid (*Platanthera praeclara*) at the northern
- 500 limit of its range in Manitoba, Canada. Am Midl Nat 174:191–203. doi: 10.1674/0003-0031-

501 174.2.191

- Bontadina F, Arlettaz R, Fankhauser T, et al (2000) The lesser horseshoe bat *Rhinolophus hipposideros* in Switzerland: present status and research recommendations. Le Rhinolophe
  14:69–83.
- 505 Bontadina F, Schofield H, Naef-Daenzer B (2002) Radio-tracking reveals that lesser
- horseshoe bats (*Rhinolophus hipposideros*) forage in woodland. J Zool 258:281–290. doi:
  10.1017/S0952836902001401
- Bruggeman JE, Swem T, Andersen DE, et al (2015) Dynamics of a recovering arctic bird
  population: the importance of climate, density dependence, and site quality. Ecol Appl
  25:1932–1943.
- Burles DW, Brigham RM, Ring RA, Reimchen TE (2009) Influence of weather on two
  insectivorous bats in a temperate Pacific Northwest rainforest. Can J Zool 87:132–138.

- 513 Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical
- 514 information-theoretic approach. Springer
- 515 Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel
- 516 inference in behavioral ecology: some background, observations, and comparisons. Behav
- 517 Ecol Sociobiol 65:23–35. doi: 10.1007/s00265-010-1029-6
- 518 Calcagno V, de Mazancourt C, et al (2010) glmulti: an R package for easy automated model
- selection with (generalized) linear models. J Stat Softw 34:1–29.
- 520 Ceglar A, Toreti A, Lecerf R, et al (2016) Impact of meteorological drivers on regional inter-
- annual crop yield variability in France. Agric For Meteorol 216:58–67. doi:
- 522 10.1016/j.agrformet.2015.10.004
- 523 Ciechanowski M, Zajac T, Bilas A, Dunajski R (2007) Spatiotemporal variation in activity of
- 524 bat species differing in hunting tactics: effects of weather, moonlight, food abundance, and
- structural clutter. Can J Zool 85:1249–1263.
- 526 Ciuti S, Jensen WF, Nielsen SE, Boyce MS (2015) Predicting mule deer recruitment from
- 527 climate oscillations for harvest management on the northern Great Plains: Predicting deer
- recruitment from climate indices. J Wildl Manag 79:1226–1238. doi: 10.1002/jwmg.956
- 529 Del Toro I, Silva RR, Ellison AM (2015) Predicted impacts of climatic change on ant
- 530 functional diversity and distributions in eastern North American forests. Divers Distrib
- 531 21:781–791. doi: 10.1111/ddi.12331
- 532 Delignette-Muller ML, Dutang C (2014) fitdistrplus: An R Package for fitting distributions. J
  533 Stat Softw 64:1–34.

- 534 Dool SE, Puechmaille SJ, Dietz C, et al (2013) Phylogeography and postglacial recolonization
- of Europe by *Rhinolophus hipposideros*: evidence from multiple genetic markers. Mol Ecol
- 536 22:4055–4070. doi: 10.1111/mec.12373
- 537 Dool SE, Puechmaille SJ, Kelleher C, et al (2016) The effects of human-mediated habitat
- 538 fragmentation on a sedentary woodland-associated species (*Rhinolophus hipposideros*) at its
- range margin. Acta Chiropterol 18:377–393.
- 540 Dugger KM, Forsman ED, Franklin AB, et al (2016) The effects of habitat, climate, and
- 541 Barred Owls on long-term demography of Northern Spotted Owls. The Condor 118:57–116.
- 542 doi: 10.1650/CONDOR-15-24.1
- Forrester TD, Wittmer HU (2013) A review of the population dynamics of mule deer and
  black-tailed deer *Odocoileus hemionus* in North America. Mammal Rev 43:292–308. doi:
  10.1111/mam.12002
- 546 Frick WF, Reynolds DS, Kunz TH (2010) Influence of climate and reproductive timing on
- 547 demography of little brown myotis *Myotis lucifugus*. J Anim Ecol 79:128–136. doi:
- 548 10.1111/j.1365-2656.2009.01615.x
- 549 Frick WF, Stepanian PM, Kelly JF, et al (2012) Climate and weather impact timing of
- emergence of bats. PLoS ONE 7:e42737. doi: 10.1371/journal.pone.0042737
- 551 Gaisler J (1966) Reproduction in the lesser horseshoe bat (*Rhinolophus hipposideros*
- *hipposideros* Bechstein, 1800). Bijdr Tot Dierkd 36:45–62.
- 553 Geber MA (2008) To the edge: studies of species' range limits. New Phytol 178:228–230.

- Gedir JV, Cain JW, Harris G, Turnbull TT (2015) Effects of climate change on long-term
  population growth of pronghorn in an arid environment. Ecosphere 6:1-20. doi:
  10.1890/ES15-00266.1
- 557 Giam X, Olden JD (2016) Quantifying variable importance in a multimodel inference
- 558 framework. Methods Ecol Evol 7:388–397. doi: 10.1111/2041-210X.12492
- Griffin DR (1971) The importance of atmospheric attenuation for the echolocation of bats(Chiroptera). Anim Behav 19:55–61.
- 561 Grindal SD, Collard TS, Brigham RM, Barclay RM (1992) The influence of precipitation on
- reproduction by *Myotis* bats in British Columbia. Am Midl Nat 128:339–344.
- 563 Hasan F, Ansari MS (2016) Temperature-dependent development and demography of
- 564 Zygogramma bicolorata (Coleoptera: Chrysomelidae) on Parthenium hysterophorus. Ann
- 565 Appl Biol 168:81–92. doi: 10.1111/aab.12244
- 566 Haysom K, Dekker J, Russ J, et al (2013) European bat population trends a prototype
- 567 biodiversity indicator. European Environment Agency
- 568 Herfindal I, van de Pol M, Nielsen JT, et al (2015) Climatic conditions cause complex
- 569 patterns of covariation between demographic traits in a long-lived raptor. J Anim Ecol
- 570 84:702–711. doi: 10.1111/1365-2656.12318
- 571 Hoying KM, Kunz TH (1998) Variation in size at birth and post-natal growth in the
- 572 insectivorous bat *Pipistrellus subflavus* (Chiroptera: Vespertilionidae). J Zool 245:15–27.
- 573 Hoyle SD, Pople AR, Toop GJ (2001) Mark–recapture may reveal more about ecology than
- about population trends: demography of a threatened ghost bat (*Macroderma gigas*)
- 575 population. Austral Ecol 26:80–92.

- 576 Jones G, Jacobs DS, Kunz TH, et al (2009) Carpe noctem: the importance of bats as
- 577 bioindicators. Endanger Species Res 8:93–115.
- 578 Kanno Y, Pregler KC, Hitt NP, et al (2016) Seasonal temperature and precipitation regulate
- 579 brook trout young-of-the-year abundance and population dynamics. Freshw Biol 61:88–99.
- 580 doi: 10.1111/fwb.12682
- 581 Kayikcioglu A, Zahn A (2004) High temperatures and the use of satellite roosts in
- 582 *Rhinolophus hipposideros*. Mamm Biol 69:337–341. doi: 10.1078/1616-5047-00152
- 583 Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and
- spatial data to predict species' ranges. Ecol Lett 12:334–350.
- 585 Kearney MR, Matzelle A, Helmuth B (2012) Biomechanics meets the ecological niche: the
- importance of temporal data resolution. J Exp Biol 215:1422–1424. doi: 10.1242/jeb.072249
- 587 Kerbiriou C, Julien JF, Monsarrat S, et al (2015) Information on population trends and
- 588 biological constraints from bat counts in roost cavities: a 22-year case study of a pipistrelle
- 589 bats (*Pipistrellus pipistrellus Schreber*) hibernaculum. Wildl Res 42:35. doi:
- 590 10.1071/WR14197
- 591 Kingsolver JG (1989) Weather and the population dynamics of insects: integrating
- 592 physiological and population ecology. Physiol Zool 62:314–334.
- 593 Lamy C, Dubreuil V (2010) Impact des sécheresses en bretagne sur le bilan hydrique:
- 594 modélisation à partir du climat d'années passées 23ème Colloque de l'Association
- 595 Internationale de Climatologie, pp 325–330

Leigh C, Bush A, Harrison ET, et al (2015) Ecological effects of extreme climatic events on
riverine ecosystems: insights from Australia. Freshw Biol 60:2620–2638. doi:

598 10.1111/fwb.12515

- 599 Link WA, Barker RJ (2006) Model weights and the foundations of multimodel inference.
- 600 Ecology 87:2626–2635.
- 601 López-Roig M, Serra-Cobo J (2014) Impact of human disturbance, density, and
- 602 environmental conditions on the survival probabilities of pipistrelle bat (*Pipistrellus*
- 603 *pipistrellus*). Popul Ecol 56:471–480. doi: 10.1007/s10144-014-0437-2
- Lučan RK, Weiser M, Hanák V (2013) Contrasting effects of climate change on the timing of
- reproduction and reproductive success of a temperate insectivorous bat: Climate change and
- reproduction of a temperate bat. J Zool 290:151–159. doi: 10.1111/jzo.12021
- 607 Lukacs PM, Burnham KP, Anderson DR (2010) Model selection bias and Freedman's
- 608 paradox. Ann Inst Stat Math 62:117–125. doi: 10.1007/s10463-009-0234-4
- 609 Masciocchi M, Pereira AJ, Corley JC (2016) Local dynamics of worker activity of the
- 610 invasive *Vespula germanica* and *V. vulgaris* (Hymenoptera: Vespidae) wasps in Argentina:
- 611 Activity fluctuations of *Vespula* spp. in Argentina. Ecol Entomol 41:105–111. doi:
- 612 10.1111/een.12277
- 613 McLean N, Lawson CR, Leech DI, van de Pol M (2016) Predicting when climate-driven
- 614 phenotypic change affects population dynamics. Ecol Lett. 19:595-608. doi:
- 615 10.1111/ele.12599
- 616 Metz J, Tielboerger K (2016) Spatial and temporal aridity gradients provide poor proxies for
- 617 plant-plant interactions under climate change: a large-scale experiment. Funct Ecol 30:20–29.
- 618 doi: 10.1111/1365-2435.12599

- Møller AP, Jennions MD (2002) How much variance can be explained by ecologists and
  evolutionary biologists? Oecologia 132:492–500.
- 621 Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining  $R^2$  from
- 622 generalized linear mixed-effects models. Methods Ecol Evol 4:133–142. doi: 10.1111/j.2041-
- 623 210x.2012.00261.x
- 624 Nouvellet P, Newman C, Buesching CD, Macdonald DW (2013) A Multi-metric approach to
- 625 investigate the effects of weather conditions on the demographic of a terrestrial mammal, the
- 626 european badger (*Meles meles*). PLoS ONE 8:e68116. doi: 10.1371/journal.pone.0068116
- 627 O'Hara RB, Kotze DJ (2010) Do not log-transform count data. Methods Ecol Evol 1:118–
- 628 122. doi: 10.1111/j.2041-210X.2010.00021.x
- 629 Parent CJ, Hernández F, Brennan LA, et al (2016) Northern bobwhite abundance in relation to
- 630 precipitation and landscape structure: Mapping Northern bobwhite. J Wildl Manag 80:7–18.
- 631 doi: 10.1002/jwmg.992
- Pebesma EJ (2004) Multivariable geostatistics in S: the gstat package. Comput Geosci
  30:683–691.
- 634 Peterman WE, Semlitsch RD (2014) Spatial variation in water loss predicts terrestrial
- salamander distribution and population dynamics. Oecologia 176:357–369. doi:
- 636 10.1007/s00442-014-3041-4
- 637 Pretzlaff I, Kerth G, Dausmann KH (2010) Communally breeding bats use physiological and
- 638 behavioural adjustments to optimise daily energy expenditure. Naturwissenschaften 97:353–
- 639 363. doi: 10.1007/s00114-010-0647-1

- 640 Puechmaille SJ, Petit EJ (2007) Empirical evaluation of non-invasive capture-mark-recapture
- 641 estimation of population size based on a single sampling session: Non-invasive capture-mark-
- 642 recapture. J Appl Ecol 44:843–852. doi: 10.1111/j.1365-2664.2007.01321.x
- 643 Radchuk V, Johst K, Groeneveld J, et al (2014) Appropriate resolution in time and model
- 644 structure for population viability analysis: Insights from a butterfly metapopulation. Biol
- 645 Conserv 169:345–354. doi: 10.1016/j.biocon.2013.12.004
- 646 Ray D, Behera MD, Jacob J (2016) Predicting the distribution of rubber trees (*Hevea*
- 647 *brasiliensis*) through ecological niche modelling with climate, soil, topography and
- 648 socioeconomic factors. Ecol Res 31:75–91. doi: 10.1007/s11284-015-1318-7
- 649 Rebelo H, Tarroso P, Jones G (2010) Predicted impact of climate change on European bats in
- relation to their biogeographic patterns. Glob Change Biol 16:561–576.
- 651 Reiter G (2004a) Postnatal growth and reproductive biology of *Rhinolophus hipposideros*
- 652 (Chiroptera: Rhinolophidae). J Zool 262:231–241. doi: 10.1017/S0952836903004588
- 653 Reiter G (2004b) The importance of woodland for *Rhinolophus hipposideros* (Chiroptera,
- 654 Rhinolophidae) in Austria. Mamm Mamm 68:403–410.
- 655 Saether BE, Sutherland WJ, Engen S (2004) Climate influences on avian population
- dynamics. In: Moller AP, Fielder W, Berthold P (eds) Birds and climate change. Elsevier
- 657 Science Ltd, London, pp 185–209
- 658 Sæther B-E, Tufto J, Engen S, et al (2000) Population dynamical consequences of climate
- change for a small temperate songbird. Science 287:854–856. doi:
- 660 10.1126/science.287.5454.854

- Satterthwaite WH, Kitaysky AS, Mangel M (2012) Linking climate variability, productivity
  and stress to demography in a long-lived seabird. Mar Ecol Prog Ser 454:221–235. doi:
  10.3354/meps09539
- 664 Schorcht W, Bontadina F, Schaub M (2009) Variation of adult survival drives population
- dynamics in a migrating forest bat. J Anim Ecol 78:1182–1190. doi: 10.1111/j.1365-

666 2656.2009.01577.x

- 667 Seckerdieck A, Walther B, Halle S (2005) Alternative use of two different roost types by a
- 668 maternity colony of the lesser horseshoe bat (*Rhinolophus hipposideros*). Mamm Biol
- 669 70:201–209. doi: 10.1016/j.mambio.2004.10.002
- 670 Şekercioğlu ÇH, Primack RB, Wormworth J (2012) The effects of climate change on tropical
- 671 birds. Biol Conserv 148:1–18. doi: 10.1016/j.biocon.2011.10.019
- 672 Spiller DA, Schoener TW (2008) Climatic control of trophic interaction strength: the effect of
- 673 lizards on spiders. Oecologia 154:763–771. doi: 10.1007/s00442-007-0867-z
- Taylor LR (1963) Analysis of the effect of temperature on insects in flight. J Anim Ecol
- 675 32:99–117. doi: 10.2307/2520
- Thomas CD, Cameron A, Green RE, et al (2004) Extinction risk from climate change. Nature
  427:145–148.
- Thomas JA, Moss D, Pollard E (1994) Increased fluctuations of butterfly populations towards
- the northern edges of species' ranges. Ecography 17:215–220. doi: 10.1111/j.1600-
- 680 0587.1994.tb00096.x

- Townsend AK, Cooch EG, Sillett TS, et al (2016) The interacting effects of food, spring
- temperature, and global climate cycles on population dynamics of a migratory songbird. Glob
- 683 Change Biol 22:544–555. doi: 10.1111/gcb.13053
- Turner MG, Dale VH, Gardner RH (1989) Predicting across scales: theory development and
- testing. Landsc Ecol 3:245–252.
- 686 Uhrin M, Hüttmeir U, Kipson M, et al (2016) Status of Savi's pipistrelle Hypsugo savii
- 687 (Chiroptera) and range expansion in Central and south-eastern Europe: a review. Mammal
- 688 Rev 46:1–16. doi: 10.1111/mam.12050
- 689 Urban MC, Bocedi G, Hendry AP, et al (2016) Improving the forecast for biodiversity under
- climate change. Science 353:1113. doi: 10.1126/science.aad8466
- 691 Van de Pol M, Bailey LD, McLean N, et al (2016) Identifying the best climatic predictors in
- ecology and evolution. Methods Ecol Evol. doi: 10.1111/2041-210X.12590
- 693 Van de Pol M, Vindenes Y, Sæther B-E, et al (2010) Effects of climate change and variability
- on population dynamics in a long-lived shorebird. Ecology 91:1192–1204.
- 695 Van der Wal J, Beaumont L, Zimmerman N, Lorch P (2014) Climates: methods for working
- 696 with weather & climate. R package version 0.1-1.6.
- 697 Voigt CC, Schneeberger K, Voigt-Heucke SL, Lewanzik D (2011) Rain increases the energy
- 698 cost of bat flight. Biol Lett 7:793–795. doi: 10.1098/rsbl.2011.0313
- 699 White TCR (2008) The role of food, weather and climate in limiting the abundance of
- 700 animals. Biol Rev 83:227–248. doi: 10.1111/j.1469-185X.2008.00041.x
- 701 Williams CB (1951) Changes in insect populations in the field in relation to preceding
- weather conditions. Proc R Soc Lond B Biol Sci 138:130–156. doi: 10.1098/rspb.1951.0011

- 703 Wu J (2016) Detection and attribution of the effects of climate change on bat distributions
- over the last 50 years. Clim Change 134:681–696. doi: 10.1007/s10584-015-1543-7
- Xu T, Hutchinson MF (2013) New developments and applications in the ANUCLIM spatial
- climatic and bioclimatic modelling package. Environ Model Softw 40:267–279. doi:
- 707 10.1016/j.envsoft.2012.10.003
- Zahn A (1999) Reproductive success, colony size and roost temperature in attic-dwelling bat
   *Myotis myotis*. J Zool 247:275–280.
- 710 Zuur AF, Ieno EN, Walker NJ, et al (2009) Zero-truncated and zero-inflated models for count
- data. In: Mixed effects models and extensions in ecology with R. Springer New York, pp
- 712 261–293

#### 713 Data Accessibility:

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

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

			Monthly models	S	Life cycle models			Yearly models		
		Aver. Temp.	Min. Temp.	Precip.	Aver. Temp.	Min. Temp.	Precip.	Aver. Temp.	Min. Temp.	Precip.
	August	NS	NS	NS						
	September	NS	NS	NS						
Mating	October	NS	NS	-	NS	NS	NS			
	November	+	+	NS	_					
	December	NS	NS	NS		NS	NS	NC	NS	NS
Hibernation	January	NS	NS	NS	NS					
	February	NS	NS	NS				113	NS	113
Corion	March	NS	NS	NS						
Spring Transition	April	NS	NS	NS	NS	NS	NS			
Transition	May	+	+	NS						
Parturition	June	NS	NS	+	NC	NIC	· · · · · ·			
	July	NS	NS	NS	- 103	NS III	Ŧ			
AIC - Significa	int predictor	5748.96	5749.26	5743.98	NA	NA	5751.2	5757.36	5757.42	5757.36
(Rar	nk)	(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 model	s	Yearly models					
		Aver. Temp.	Min. Temp.	Precip.	Aver. Temp.	Min. Temp.	Precip.	Aver. Temp.	Min. Temp.	Precip.			
	August	NS	NS	NS									
	September	NS	NS	NS			+						
Mating	October	NS	NS	+	NS	NS							
	November	NS	NS	NS	-								
	December	NS	NS	NS	NS NS	NS		- NS -	NS	NS			
Hibernation	January	NS	NS	NS			NS						
	February	NS	NS	NS									
Carriera	March	NS	NS	NS									
Spring	April	+	+	-	NS	+	+	+	+	NS			
Transition	May	NS	NS	NS	-								
Darturition	June	NS	NS	NS	NC	NC	NC	_					
Partuntion	July	+	+	NS	- 113	103	112						
AIC - Significa	nt predictor	-55.24	-61.35	-57.55	NA	-42.24	-47.25	-35.60	-38.34	-35.79			
(Rar	nk)	(3)	(1)	(2)		(5)	(4)	(8)	(6)	(7)			

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

	Variable Description	Number (BIOCLIM)	Significance	Significant predictors	
	Annual mean temperature	1	NS		
	Mean diurnal range	2	NS		
	Isothermality (2/7)	3			
e	Temperature seasonality	4	NS		
atur	Maximum temperature of warmest month	5	NS		
pera	Minimum temperature of coldest month	6	+	-37.78	
em	Temperature annual range (5-6)	7			
F	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		
	Annual precipitation	12	-		
	Precipitation of wettest month	13	NS		
ion	Precipitation of driest month	14	NS		
itat	Precipitation seasonality	15	-	-13 30	
ecip	Precipitation of wettest quarter	16	+	-43.50	
Рге	Precipitation of driest quarter	17	NS		
	Precipitation of the warmest quarter				
	Precipitation of the coldest quarter	19	NS		

### **Table 4**: AIC and ranks of models that included both minimum temperature and precipitation significant predictors for the different temporal

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
	Month	Minimum temperature : April & July Precipitation : October & April	65.14 (1)	0.053	0.177
Idity	Life cycle	Minimum temperature : Spring Transition Precipitation : Mating	-51.79 (2)	0.027	0.154
Fecur	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**

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

738 Figure 1

