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**Information on population trends and biological constraints from bat counts in roost cavities: a twenty-two-year case study of a Pipistrelle bats (*Pipistrellus pipistrellus*, Schreber) hibernaculum.**

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1 **Title:** Information on population trends and biological constraints from bat counts in roost  
2 cavities: a twenty-two-year case study of a Pipistrelle bats (*Pipistrellus pipistrellus*, Schreber)  
3 hibernaculum.

4  
5 **Running head:** Pragmatic approach to analyse count data of bats in hibernaculum  
6

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23 **Words count:** 5902  
24

25 **Abstract** (Words count: 349)

26 **Context:** According to the current trend of biodiversity loss, information on population trends at  
27 large temporal and spatial scales is necessary. However, well-documented animal population  
28 dynamics are generally based on intensive protocols requiring animal manipulation, which can  
29 be impossible to conduct in species for which conservation is a concern.

30 **Aims:** For many bat species, an alternative approach entails performing an appropriate analysis  
31 of counts in roost cavities. Because of managers' perception of chaotic variations through time,  
32 relatively few count monitoring surveys are regularly analysed. Here, we present the analysis of  
33 a twenty-two-year survey of a large hibernaculum of pipistrelle bats (*Pipistrellus pipistrellus*)  
34 located in a railway tunnel in Paris, France.

35 **Methods:** We propose that using combinations of population dynamics modelling using  
36 demographic parameters from the literature and statistical analyses helps with identifying the  
37 biological and methodological effects underlying the dynamics observed in census analyses.

38 **Key results:** we determined that some of the observed year-to-year variations of population size  
39 cannot be explained only by the intrinsic dynamics of the population. In particular, in 1993-  
40 1994, the population size increased by >40%, which should have implied a massive immigration.  
41 This change coincided with the end of the operation of the railway line. After consideration of a  
42 drastic trend of population decline (7%/year) we were able to detect this event and several  
43 environmental effects. Specifically, the winter conditions and the temperature in July affected  
44 the colony size, presumably because of aggregative behavior and reproduction success,  
45 respectively.

46 **Conclusions:** Emigration-immigration processes might have preponderant effects on population  
47 dynamics. In addition, we our analysis demonstrates that (1) the study population suffered a  
48 large decline (2) a combination of human disturbance and meteorological variation explains

49 these dynamics; (3) Emigration-immigration processes have preponderant effects on the  
50 population dynamics,

51 **Implications:** To conduct a meaningful analysis of non standard time series and provide a source  
52 of data for implementing biodiversity indicators, it is necessary to include (1) the local  
53 knowledge of the people involved in the field surveys in these analyses (the existence of  
54 disturbances and site protections) and (2) meteorological information for the appropriate  
55 seasons of the year.

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## 61 **Key words**

62 *Pipistrellus pipistrellus*; Population dynamics; count monitoring; deterministic matrix model;

63 Stochastic-individual-based population model; disturbance

64

65

## 66 **Introduction**

67 In the current context of the drastic erosion of biodiversity, “*unprecedented additional efforts*  
68 *would be needed to achieve a significant reduction in the rate of biodiversity loss at all levels*”  
69 (Biodiversity Synthesis of the Millennium Ecosystem Assessment (MEA 2005). To reach this  
70 target, the efforts undertaken by each country should be assessed. In Europe, the  
71 implementation of the Convention on Biological Diversity has been outlined by the Streamlining  
72 European Biodiversity Indicators (SEBI) initiative that proposes a first set of indicators to  
73 monitor the progress in Europe (European Environment Agency, 2009). The first set of this  
74 indicator can be considered “direct” core biodiversity indicators based on population trends  
75 and the diversity of a group of species (Balmford *et al.* 2005) or the Red List Index (Butchart *et*  
76 *al.* 2005).

77 Well-documented animal population dynamics studies are generally based on quantitative  
78 methods allowing unbiased and independent estimations of survival, fecundity and dispersal  
79 rates and subsequent projection modelling using these specific rates (Beissinger and  
80 McCullough 2002). However, the acquisition of such data requires intensive protocols (e.g.,  
81 capture-mark-recapture protocols to estimate survival and/or dispersal rates). These methods,  
82 often involving animal handling, such as capture-recapture, could be controversial approaches  
83 when the species are endangered and/or sensitive to disturbance and could also affect the  
84 results (Saraux *et al.* 2011), particularly with regard to bats (Punt 1970; Dietz *et al.* 2006). In  
85 addition, such time-consuming methods require highly qualified personnel and can hardly be  
86 extended to a large number of sites and species.

87

88 Most of the European bat populations have a poor conservation status because of various  
89 pressures, such as the loss of suitable foraging habitats (Walsh and Harris 1996; Kunz and

90 Fenton 2003), agricultural intensification (Swanepoel *et al.* 1999; Wickramasinghe *et al.* 2003),  
91 urbanisation (Kurta and Teramino 1992; Loeb *et al.* 2009) and forest management (O'Donnell  
92 2000). Human activities strongly reduce the availability of underground sites used by bats for  
93 breeding or/and hibernation. Whereas some underground sites are filled in, blocked up or  
94 transformed (Mitchell-Jones *et al.*, 2007), others are opened for tourism activities, resulting in  
95 recurrent disturbances. Such activities may have major consequences on the population  
96 dynamics of bat species at large scales since (1) several studies have stressed the high  
97 sensitivity of bats to human disturbance (Mc Craken 1989; Speakman *et al.* 1991; Gore *et al.*  
98 2012); (2) in some cases, the loss of a single site can affect the dynamics of bat populations over  
99 areas of several thousands of square kilometers (Mitchell-Jones *et al.* 2007). Within this  
100 context, an increasing number of bat populations occurring in roost cavities are protected and  
101 regularly counted (see the Conservation Trust and Eurobat annuals reports). However, because  
102 of the managers' perception that hibernacula counts exhibit chaotic variations over time, only  
103 relatively few hibernacula counts are regularly analysed, which, in turn may lead to the  
104 abandonment of such monitoring. Nevertheless, efforts have been made to analyse count data  
105 provided by volunteers in the context of breeding roost surveys and to provide sound  
106 assessment of population trends (Warren and Witter 2002). Less effort has been devoted so far  
107 to hibernaculum monitoring, despite the availability of hibernaculum count data and the  
108 need for conservationists to detect population declines when formulating management  
109 decisions (Trombulak *et al.* 2001; Frick *et al.* 2010). O'Shea *et al.* (2003) advocated that new  
110 techniques must be explored and modern statistical designs applied in order to improve the  
111 scientific basis for conclusions about future bat population trends. Some recent studies and  
112 reports have considered hibernaculum count data to assess population variations (see  
113 Prendergast *et al.* 2010; European Environment Agency 2013)

114 A better understanding of the biological information included in these time series evaluations  
115 could allow (1) to design and propose of more efficient count protocols (e.g., which  
116 environmental variable to record at monitoring sites), (2) to detect population trends and then  
117 provide efficient biodiversity indicators, and (3) to assess the impact of management actions  
118 (such as fitting a grille across the hibernaculum entrance permitting the free passage of bats  
119 but not people, Provision of additional roosting places, etc.)

120 The purpose of this study is to investigate how simple, specific count-based datasets can be  
121 used in combination with standard ecological methods and generic demographic data to  
122 understand the processes underlying the observed population dynamics. If count data from  
123 roosts in winter can be considered as a reliable proxy of a local population's size (for sedentary  
124 species), we hypothesize that we will be able to detect the effects of meteorological conditions  
125 on local population dynamics. Weather and food availability are known to be highly correlated  
126 with each other and with parturition in insectivorous bats (Arlettaz *et al.* 2011), which is in turn  
127 related with reproductive success and survival of newly volant young (Tuttle 1976). Therefore,  
128 during the reproductive period, local bad weather conditions such as low temperature or  
129 important rainfall should affect the reproductive success and then impact negatively population  
130 size in winter, and, subsequently, count data. However, if population dynamics are only  
131 assessed through roost count data (and not with e.g., variation in demographic parameters),  
132 meteorological effects may be masked by (1) a population trend (such as a large decline), (2) an  
133 aggregative behavior linked with winter condition (Mumford 1958; Sandel *et al.* 2001) and (3)  
134 human disturbance.

135 Local population dynamics do not only rely on intrinsic processes (mortality and fecundity) but  
136 may also be more or less strongly influenced by immigration or emigration processes. Although  
137 disentangling the roles of intrinsic dynamics and immigration/emigration is not possible with

138 count data, however based on a good knowledge of the species' demography it is possible to  
139 detect changes that cannot be explained only by intrinsic dynamics and involve necessary  
140 events of immigration or emigration. We first used population dynamics models with a set of  
141 generic demographic parameter values available from the literature to construct a realistic  
142 distribution of expected annual growth rates in the absence of emigration/immigration. In a  
143 second step, we compared this expected distribution (which only depends on the life history  
144 traits of the species and its capacity of intrinsic population growth) with the observed annual  
145 growth rates to detect important immigration-emigration events or local catastrophic events,  
146 such as epizootics (which is not an exclusive hypothesis) (Blehert *et al.* 2009).

147 After these exploratory steps, we conducted a statistical modelling to test the following  
148 assumptions:

149 (1) Favorable meteorological conditions such as higher temperatures during the reproductive  
150 period should positively influence counts from roost in following winter (larger number of  
151 young produced), whereas unfavorable meteorological conditions such as strong precipitation  
152 should have a negative impact. (2) Cold temperatures in winter may lead to increased counts  
153 from roosts (in the same winter), due to aggregative behavior. (3) human disturbance in the  
154 roost should adversely affect counts.

155 We believe that applying this simple approach to bat count data will allow a better  
156 understanding of the biological information contained in available time series.

157 We focused on a large population of common pipistrelle bats (*Pipistrellus pipistrellus*, Schreber)  
158 that was monitored for 22 years in an urban area.

159

## 160 **MATERIALS AND METHODS**

### 161 ***Study area***

162 From 1991 to 2012, we monitored the population size of a large hibernaculum of pipistrelle  
163 bats (*Pipistrellus pipistrellus*) located in a railway tunnel in Paris, France. This railway tunnel was  
164 in service until 1993. The bat counts were conducted in the winter by the same observers  
165 during the entire period. The counting method is a direct visual count of individuals who are  
166 located in shallow notches. These notches are expansion joint vertical depth of 10 cm between  
167 concrete slabs (see supplementary material S1). The count procedure leads thus to very thin  
168 measurements errors, because all individuals are observable. This hibernaculum is one of the  
169 most important for the species in France and the only one currently known wintering site inside  
170 the city of Paris (Lustrat and Julien 1993). Although it is possible that other unknown  
171 hibernaculums exist in Paris or in its immediate surroundings, common pipistrelles are  
172 generally found singly or in small numbers in crevices of buildings and trees in winter (Dietz *et*  
173 *al.* 2007). Thus, if existing, other hibernaculums are probably scarce and small.

#### 174 **Population dynamics modelling**

175 To discriminate between the roles of intrinsic dynamics (fecundity and mortality) and yearly  
176 emigration-immigration processes on the population dynamics, we used a combination of  
177 deterministic and stochastic models for population dynamics.

178

##### 179 *Deterministic matrix model*

180 In a first step, we used a one-sex, deterministic, age-classified Leslie-matrix model (Caswell,  
181 2001) to infer the equilibrium intrinsic population properties (in particular, the asymptotic  
182 time-invariant population growth rate). This model was implemented using the ULM software  
183 (Legendre and Clobert 1995; Ferrière *et al.* 1996). We considered a two-age class model (Fig. 1.;  
184 Sendor and Simon 2003) with the following parameter values obtained from the literature: the  
185 first reproduction occurring in the first year (Schober and Grimmberger 1998; Dietz *et al.* 2007);

186 the first year survival probability,  $s_0$ , was set to 0.53 (Sendor and Simon 2003); the adult survival  
187 probability,  $s_{ad}$ , varied from 0.37 to 0.80 (Thompson 1987; Gerell and Lundberg, 1990; Sendor  
188 and Simon 2003,) and the average female productivity,  $F$ , varied from 0.58 to 0.988 (Webb *et*  
189 *al.* 1996; Barclay *et al.* 2004). In many respects, bats have relatively slow life histories (Barclay  
190 *et al.* 2004) thus one can expect small growth rate variations and this modelling approach aims  
191 to assess a range of realistic values for annual growth rates.

192

193 *Approximate position of figure 1*

194

195 *Stochastic, individual-based population model*

196 In addition, to compare the actual observed annual growth rates with their theoretical  
197 distribution under demographic stochasticity in the absence of immigration and emigration, we  
198 developed a stochastic two-sex individual-based population model. This model allowed the  
199 complete description of all of the individuals in terms of sex and age. In each time interval  
200 (year), adult individuals were randomly paired according to a polygynous mating system with  
201 an unrestricted harem size, i.e., we assumed that all mature females present in the population  
202 can reproduce provided that there was at least one male in the population (Legendre *et al.*  
203 1999). This hypothesis is realistic, as recent results suggest that the proportion of breeding  
204 females among adult females is usually very high (about 95%, see Barclay *et al.*, 2004). The  
205 reproductive success of each pair was determined according to a Bernoulli drawing of  
206 parameter  $F$  (in cases where  $F < 1.0$ ), or a Poisson trial of parameter  $F$  (in cases where  $F \geq 1$ ). The  
207 sex of each newborn individual was randomly determined according to a 1:1 mean sex ratio.  
208 Reproduction was followed by the differential mortality of individuals according to age-specific  
209 annual survival rates ( $S_0$  and  $S_{ad}$ ). Each individual survival event was drawn from a Bernoulli

210 function. The parameters used were the same as for the deterministic matrix models. Three  
211 scenarios were considered (pessimistic, median and optimistic) using either the minimal,  
212 median or maximal values of  $S_{ad}$  and  $F$  obtained from the literature (Thompson 1987; Gerell and  
213 Lunddberg 1990; Webb *et al.* 1996; Sendor and Simon 2003; Barclay *et al.* 2004). For each  
214 scenario, the changes in the population size were investigated for 1000 independent random  
215 population trajectories drawn over a fixed time horizon (22 years). The distributions of the  
216 ratios of population size at a time  $t$  ( $N_t$ ) / population size at a time  $t-1$  ( $N_{t-1}$ ) were then  
217 compared to the observed ratios. At time zero, the population trajectories were assumed at the  
218 demographic equilibrium (stable age-class distribution and balanced sex ratio), with a total  
219 population size equal to the observed population size in 1991. In each model trajectory, years  
220 with  $N_t < 20$  individuals were excluded to avoid an inflation of the variance in the growth rates  
221 due to a strong sampling effect (see e.g., Lande *et al.* 2003), which would have precluded the  
222 comparison with the actual data (the observed population sizes were in the range of 350-1500).

223  
224 **Analysis of year-to-year variation and trend in population size. Effect of weather**  
225 **conditions and human disturbance.**

226 We examined temporal variations in the number of bats counted in the hibernaculum by (1)  
227 testing for a (decreasing or increasing) trend in numbers over the study period (1991-2012); (2)  
228 testing for an effect of the railway traffic on bat numbers. The railway tunnel was in service  
229 until 1993; since traffic can substantially affect roost attractiveness, we included this factor in  
230 our statistical analysis as a binary variable (presence or absence of railway traffic). (3) Finally, to  
231 assess the effect of weather conditions on the winter population size, we tested the existence  
232 of correlations between the count data of bat and several weather variables. Some  
233 meteorological variables, such as the winter conditions, are expected to influence hibernating

234 bat aggregation in certain favourable hibernacula, such as tunnels, which become more  
235 attractive when the conditions are extreme. Other meteorological variables, such as the  
236 precipitation or temperature levels, recorded the year before the winter bat counts were  
237 expected to influence the reproductive success and survival of young (Grindal *et al.* 1992; Zahn  
238 1999) and, thus, affect the population size the following winter. The weather data were  
239 obtained from two websites: Infoclimat and European Climate Assessment and Dataset.

240

#### 241 *Statistical analysis*

242 As we expected that some weather variables might be correlated with each other or might  
243 show trends over the period considered, we used Spearman's rank test to assess the  
244 correlation between paired samples of variables (see supplementary material S1), with the aim  
245 of avoiding the inclusion of correlated explanatory variables in statistical analyses. Weather  
246 variables in winter indeed showed strong correlations between them, as did the group of  
247 variables recorded in the spring before the winter counts (supplementary material S2). Only the  
248 variable *average temperature in June* showed a yearly significant increasing trend  
249 (supplementary material S2).

250 In a first step, we assessed the influence of each variable (yearly trend, human disturbance  
251 (railway traffic), weather conditions) on count data. In a second step, in order to take into  
252 account possible population trend that could hide the effect of human disturbance or weather  
253 conditions on bat numbers, we adjusted these variables to yearly trend using a sequential  
254 ANOVA (type I) in which the effects are tested sequentially.

255 When the variables exhibited a significant influence, we choose the variable that explained  
256 more of the deviance using the Akaike Information Criterion (AIC) for these two groups (winter  
257 variable and spring variable) because this criterion has the advantage of generality and can be

258 applied further than the normal linear models (Faraway 2006). Finally, we constructed a full  
259 model including yearly trend, railway traffic and meteorological variables and we performed an  
260 AIC-based model selection by removing variables (see supplementary material S4 for details) to  
261 test if the full model was the most parsimonious choice. We used Generalised Linear Models  
262 (GLMs) with Poisson error distribution due to the nature of the data (count) (Crawley 2009) and  
263 we account for over-dispersion following Faraway's (2006) recommendations (note that similar  
264 results were obtained with GLM with negative binomial error distribution).  
265 We also carried out an alternative approach (see supplementary material S3), in which we took  
266 into account simultaneously all variables (trend, railway traffic, weathers conditions), using  
267 Hierarchical Partitioning (HP, R package hier.part). This approach allowed us to identify the  
268 most likely causal factors of variation in bat numbers while alleviating multicollinearity  
269 problems (Mac Nally 2000).

270

## 271 **RESULTS**

### 272 **Comparison of observed growth rates and those assessed with modelling.**

273 Considering the range of demographic parameter values available in the literature, the  
274 asymptotic time-invariant population growth rate ( $\lambda$ ) given by our matrix model was between  
275 0.523 and 1.065. Moreover, increasing simultaneously demographic parameters, such as  
276 fecundity or survival, rarely led to  $\lambda > 1.4$  (Fig. 2).

277

278 *Approximate position of figure 2*

279

280 The stochastic model allowed us to obtain a distribution of annual growth rates that accounted  
281 for the random fluctuations in the population size due to demographic stochasticity under the

282 three demographically reasonable scenarios for the Pipistrelle (Fig. 3) These three contrasted  
283 scenarios are: a pessimistic scenario,  $S_0=0.53$ ,  $S_{ad}=0.37$ ,  $F=0.58$ ; a median scenario,  $S_0=0.53$ ,  
284  $S_{ad}=0.59$ ,  $F=0.78$  and an optimistic scenario,  $S_0=0.53$ ,  $S_{ad}=0.8$ ,  $F=0.99$ . The 95% confidence  
285 intervals of the annual growth rates were (0.38 - 0.66), (0.72 - 0.86), (1.01 - 1.11), respectively,  
286 for the pessimistic, median and optimistic scenarios.

287

288 *Approximate position of figure 3*

289

290 The comparison between these expectations and the observed annual growth rates indicated  
291 that some of the strong year-to-year increases ( $N_t/N_{t-1}>1.15$ ) in the population size observed in  
292 the time series cannot be explained only by the intrinsic dynamics of the population without  
293 emigration-immigration process (Fig. 3) and may have implied massive immigration events. In  
294 particular, there were two years (1993-1994 and 2008-2009, Fig. 4) in which the population size  
295 increased by >40%, presumably because of a massive immigration (see the Discussion). The  
296 increase observed between 1993 and 1994 (+384 individuals) corresponds to the abandonment  
297 of the railway line crossing the tunnel occupied by the study population. As this change is very  
298 likely related to an arrival of individuals following the increased attractiveness of the site, we  
299 only considered the 1995-2012 period in our subsequent analysis.

300

301 *Approximate position of figure 4*

302

303 We ran an additional scenario (hereafter, the adjusted scenario) by slightly modifying the set of  
304 demographic parameters of the median scenario to yield a growth rate similar to the one  
305 observed over the 1995-2012 period (details of protocol and parameters are provided in

306 supplementary material S3). This adjusted scenario ( $S_0=0.57$ ,  $S_{ad}=0.69$ ,  $F=0.84$ ) predicts that the  
307 95% confidence interval of the year-to-year growth rate should be between 0.854 and 1.013  
308 (Fig. 3). The comparison with the observed values of the growth rate during the 1995-2012  
309 period (grey circles in Fig. 3) indicates that only three of the observed growth rates are included  
310 in the confidence interval of this adjusted scenario, whereas eight are lower, and ten are  
311 higher.

312

### 313 **Population trend analyses and the importance of weather on between year** 314 **variations.**

315 Over the 1991-2012 period, we did not detect any temporal autocorrelation between the year-  
316 to-year growth rates in year  $t$  and  $t+1$  (Spearman's rank correlation test,  $P=0.18$ ), this indicates  
317 the absence of a strong bias in the bat count. Indeed, when an observer overestimates (or  
318 underestimates) bat numbers in a roost in a given year, one could expect that the estimation  
319 might be lowered (or inflated) in the next year, leading to an artefact of the alternation  
320 between the decreases and increases.

321 When considering each variable separately, only the year appeared significant, showing a  
322 negative trend (Table 1, this model explained 53% of the deviance). When the weather  
323 variables were adjusted to the year trend, most of their p-values drastically decreased  
324 (sequential ANOVA, Table 1). According to AIC values (Table 1) and the percentage of  
325 independent variance explained provided by the Hierarchical Partitioning (see supplementary  
326 material S5), the most important variable appeared to be the yearly trend, followed by  
327 presence of railway traffic, the group of winter weather variables (particularly frost day in  
328 January) and secondarily the group of summer variables. We then retained the number of frost  
329 day in January (Frost day) for the group of winter weather variables and the temperature in July

330 (T<sub>July</sub>) for the group of summer weather variables. We, thus, built a complete model in which  
331 the count data (period of 1991-2012) were explained by the Year + railway traffic + Frost day +  
332 T<sub>July</sub>. AIC-based model selection (see supplementary material S4) indicated that this full model  
333 is the most parsimonious choice. This model explained 93% of the variance in the population  
334 size (however, this high value should be considered with caution because the model is at the  
335 limit of the over-parameterization); 68% of this explained variance was explained by the year  
336 trend, 28% by the railway traffic presence or absence, 3% by number of frost day in January and  
337 less than 1% by the temperature in July of the previous year (these results are consistent with  
338 the Hierarchical Partitioning results, see supplementary material S3). The number of common  
339 Pipistrelle bats in the hibernaculum significantly declined over the period considered -1991 to  
340 2012-(Table 1,  $F_{1,19}=1416.85$ ;  $P<0.001$ ;  $\beta = -0.078$  [SE] 0.006), which corresponds to drastic trend  
341 of population decline: 7%/year. In addition, we detected a significant negative effect of the  
342 railway traffic ( $F_{1,18}=985.84$ ;  $P<0.001$ ;  $\beta = -0.781$  [SE] 0.100), a positive effect of number of frost  
343 days in January ( $F_{1,17}=116.82$ ;  $P<0.001$ ;  $\beta = 0.021$  [SE] 0.007 Fig. 5, and positive effect of  
344 temperature recorded in July the year prior to the winter bat counts,  $F_{1,16}=34.02$ ;  $P<0.001$ ;  $\beta = 0.$   
345  $0.027$  [SE] 0.018, Fig. 5).

346

347 *Approximate position of figure 5*

348

## 349 **DISCUSSION**

350 Despite the good availability of multi-site, long-term count data for several bat species  
351 (Mitchell-Jones *et al.* 2007), the dynamics of most monitored populations remain largely  
352 unexplored because of the conceptual and technical difficulties in discriminating the effects of  
353 multifactorial environmental disturbances, protocol artefacts and dispersal.

354 We propose that using combinations of population dynamics modelling even with demographic  
355 parameters from the literature and statistical analyses helps with identifying the biological and  
356 methodological effects in census analyses. Despite the managers' perception that population  
357 sizes show chaotic variations over time, we show that counts made by volunteers in  
358 hibernaculum can provide useful information on local population dynamics and on the  
359 environmental factors underlying these dynamics.

360

### 361 **Demographic processes underlying the observed local dynamics**

362 Using the demographic data from the literature (i.e., *generic* data) in combination with count  
363 and local environmental data (i.e., *specific* data) allowed us to define the realistic boundaries of  
364 local population variations due to intrinsic dynamics. Despite an early age at sexual maturity,  
365 the low annual fecundities reported in the literature lead to a relatively long generation length  
366 (3.9 years for the median scenario) and a relatively high sensitivity of the population growth  
367 rate to adult survival (elasticity values are respectively 0.73 and 0.27 for adult survival and  
368 fecundity, for the median scenario). Even when considering an optimistic demographic scenario  
369 that assumes high survival and fertility rates and including variations in the annual growth due  
370 to demographic stochasticity, our results suggest that some of the strong year-to-year increases  
371 in the population size could not have resulted merely from intrinsic dynamics (see Figs. 2 and 3)  
372 and might imply immigration events from unknown hibernacula. In particular, we suggest that  
373 the most rapid year-to-year increase in size (i.e., the 1993-1994 period) is linked to a change in  
374 the attractiveness of this hibernaculum as a result of the end of the exploitation of the railway  
375 line. This observation underlines the impact of disturbance on the population sizes of  
376 hibernating bats. Many studies have shown the importance of disturbance on colony dynamics  
377 and sustainability (Mc Craken 1989; Speakman *et al.* 1991; Simon *et al.* 2004; Mitchell-Jones *et*

378 *al.* 2007). The very short time delay between the end of the disturbance and its consequence  
379 on the population dynamics underlines the very active prospecting behavior of bats in choosing  
380 a favourable hibernaculum each winter (see Simon *et al.* 2004). More generally, our analysis of  
381 an adjusted scenario (which uses median demographic data from the literature that was  
382 modified to fit the growth rate observed during the 1995-2012 period) suggests that  
383 emigration-immigration processes might have preponderant effects on population dynamics.  
384 With such an approach we were able to detect that some strong year-to-year increases could  
385 not have resulted only from intrinsic dynamics and implied immigration events. However, for  
386 smaller increases that were consistent with the maximum intrinsic population growth, we were  
387 not able to distinguish the roles of intrinsic growth and immigration. Moreover, strong year-to-  
388 year reduction in population size can be related to either strong mortality or massive  
389 emigration, with little opportunity to distinguish the source of this variation.

390

### 391 **Population trends and environmental effects**

392 After removing the drastic trend of population decline (7%/year) over the 1991-2012 period,  
393 we detected a negative effect of the railway traffic on number of common pipistrelles and we  
394 further revealed some effects of the winter and summer temperatures. However the incidence  
395 of meteorological variable is very thin compare to yearly trend and presence of railway traffic.  
396 The winter effect is presumably associated with aggregation in favourable hibernacula when  
397 the winter conditions are severe, which suggests that common pipistrelles might be able to  
398 shift their winter site within the hibernating season. Several counts within the winter could,  
399 therefore, bring useful information on the extent of movements between cavities.  
400 Furthermore, correlations between the winter weather conditions and population variations  
401 within the cavity network could inform us about the specific role of each type of cavity. The

402 slightly positive influence of the temperature and slightly negative effect of rainfall during the  
403 month of July (note that  $T_{July}$  and  $P_{July}$  are not correlated) is more likely linked with reproductive  
404 parameters (i.e., fledging success or/and the survival of young). This observation fit well with  
405 the Pipistrelle's cycle of life: July is a crucial period because it corresponds to fledging of young  
406 Pipistrelle and the dispersal of the breeding colony (Arthur and Lemaire 2009).  
407 Importantly, these two seasonal environmental effects were not significantly correlated with  
408 the yearly trend, which emphasises that the observed decline of the pipistrelle population is  
409 not only explained by yearly climate variations.

410

#### 411 **Limitations and perspectives**

412 Tuttle (2003) underlined that complete enumeration of hibernating bats is possible in situations  
413 where numbers of bats are not extremely large and cavities lack great surface irregularities. In  
414 larger hibernacula with bats in roosting dense clusters, the only feasible techniques involve  
415 estimating individual densities (Thomas and Laval 1988). However, the reliability of such  
416 techniques is still unknown (Tuttle 2003). In addition to the differences in habitat  
417 characteristics, different species of bat exhibit different behaviors in winter. Some species are  
418 easily detectable, such as *Rhinolophus ssp* (which hibernates suspended to ceiling), whereas  
419 other species such as *Myotis daubentonii*, *M. bechsteinii* and *M. nattereri* hibernate in deep  
420 cracks and are less detected. The hibernaculum studied here is an ideal case since available  
421 slots are standardized (joints between concrete slabs), which allows detecting almost all  
422 individuals.

423 We did not consider immigration-emigration in our population dynamics models, since we had  
424 no means to add realistic constraints to immigration and emigration rates. Unlike the intrinsic  
425 dynamics, which are limited by biological, species-specific constraints (i.e., maximum

426 reproductive output of the species), immigration-emigration processes mainly depend on the  
427 context of the focal population (e.g., distance to other populations). Such wider context could  
428 be examined through a meta-population approach in which surrounding populations  
429 interacting with the focal one are explicitly modelled (in such case, emigration would be  
430 constrained by the available pool of migrants in the meta-population). Although our dataset  
431 does not allow us such larger scale modelling for the moment, current national hibernation  
432 surveillance scheme could provide such information in the future.

### 433 **Recommendations**

434 To conduct a meaningful analysis of time-series count data of bat in hiberculatum, it is  
435 necessary

436 (i) to include the local knowledge of the people involved in the field surveys in the analyses, for  
437 example, information on the existence of disturbances (the type, magnitude and frequency) or  
438 the implementation of site protection measures should be recorded and integrated with the  
439 count data;

440 (ii) to include the winter weather conditions, which are very likely associated with aggregation  
441 behavior (e.g., the number of frost day in January, the average temperature of January),  
442 although they do not necessarily imply demographic consequences;

443 (iii) to include the spring-summer weather information collected during the season before the  
444 winter counts (e.g., the July rainfall), as such data are expected to affect reproductive  
445 parameters, which might, in turn, influence population dynamics and

446 (iv) our analysis also strongly suggests that a multi-site approach using count data might allow  
447 strong inferences to be drawn on the intrinsic and environmental processes underlying  
448 dispersal and population dynamics.

449

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454

455

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591

592 **Table 1:** Effects of disturbance and meteorological variables on the estimates of number of bat.  
593  $T_{\text{day}}$  is the local ambient temperature at the time of the count;  $T_{\text{January}}$  is the average  
594 temperature in January;  $T_{\text{winter}}$  is the average temperature in winter (December-January-  
595 February);  $T_{\text{Anomalies}}$  is the temperature anomaly observed in January relative to the average  
596 temperatures over the 1951-1989 period; *Frost day* is the number of frost days in January;  $P_{\text{June}}$   
597 is the rainfall recorded in June of the previous year;  $P_{\text{July}}$  is the rainfall recorded in July of the  
598 previous year;  $T_{\text{June}}$  is the average temperature in June of the previous year;  $T_{\text{July}}$  is the average  
599 temperature in July of the previous year; Slope of the effect ( $\beta$ ) are given for significant test.

600

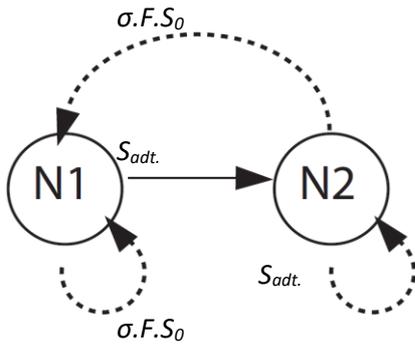
	Year	Traffic railway	Winter variables					Summer variables			
			$T_{\text{day}}$	$T_{\text{January}}$	$T_{\text{winter}}$	$T_{\text{Anomalies}}$	Frost day	$P_{\text{June}}$	$P_{\text{July}}$	$T_{\text{June}}$	$T_{\text{July}}$
<i>Effect of each variable</i>	$Z=-4.753$ $P<0.0001$ $\beta=-0.046$ $AIC=1574$	$Z=-0.085$ $P=0.93$ $AIC=3154$	$Z=0.34$ $P=0.74$ $AIC=3083$	$Z=-0.68$ $P=0.50$ $AIC=1574$	$Z=0.73$ $P=0.47$ $AIC=2907$	$Z=0.06$ $P=0.54$ $AIC=2467$	$Z=0.66$ $P=0.51$ $AIC=2922$	$Z=0.41$ $P=0.69$ $AIC=3130$	$Z=-0.04$ $P=0.97$ $AIC=3155$	$Z=-1.39$ $P=0.16$ $AIC=1574$	$Z=0.09$ $P=0.92$ $AIC=3153$
<i>Effect of each variable after adjustment to the year effect</i>	$F_{1,19}=955.6$ 3 $P<0.001$ $\beta=-0.754$ $AIC=621$	$F_{1,18}=36.11$ $P<0.0001$ $\beta=-0.009$ $AIC=1532$ $AIC=621$	$F_{1,19}=106.0$ 1 $P<0.0001$ $\beta=-0.043$ $AIC=1470$	$F_{1,19}=35.18$ $P<0.0001$ $\beta=-0.037$ $AIC=1533$	$F_{1,16}=5.95$ $P=0.015$ $\beta=-0.037$ $AIC=1529$	$F_{1,16}=113.81$ $P<0.0001$ $\beta=0.021$ $AIC=1454$	$F_{1,19}=16.01$ $P<0.0001$ $\beta=-0.001$ $AIC=1558$	$F_{1,19}=16.01$ $P<0.0001$ $\beta=-0.001$ $AIC=1560$	$F_{1,19}=144.3$ 2 $P<0.0001$ $\beta=0.088$ $AIC=1432$	$F_{1,19}=12.19$ $P=0.001$ $\beta=0.017$ $AIC=1564$	
<i>Effect of each variable after adjustment to the year effect and railway traffic</i>		$F_{1,17}=15.65$ $P<0.0001$ $\beta=-0.006$ $AIC=597$	$F_{1,18}=83.35$ $P<0.0001$ $\beta=-0.038$ $AIC=539$	$F_{1,17}=31.96$ $P<0.0001$ $\beta=-0.037$ $AIC=552$	$F_{1,15}=1.482$ $P=0.22$ $AIC=553$	$F_{1,17}=116.82$ $P<0.0001$ $\beta=0.020$ $AIC=467$	$F_{1,18}=0.05$ $P=0.82$ $AIC=622$	$F_{1,18}=16.56$ $P<0.0001$ $\beta=-0.001$ $AIC=606$	$F_{1,18}=0.07$ $P=0.79$ $AIC=622$	$F_{1,18}=19.63$ $P<0.0001$ $\beta=0.019$ $AIC=603$	

601

602

603  
604 **Figure 1:** Life cycle of the common pipistrelle (*Pipistrellus pipistrellus*) modelled with Leslie's  
605 matrix, where  $N_i$  is the number of individuals of age,  $i$ ,  $\sigma$  is the sex ratio,  $F$  is the female  
606 fecundity (number of young emancipated per female),  $S_0$  is the first year survival probability  
607 and  $S_{adt.}$  is the survival probability of adults.

608

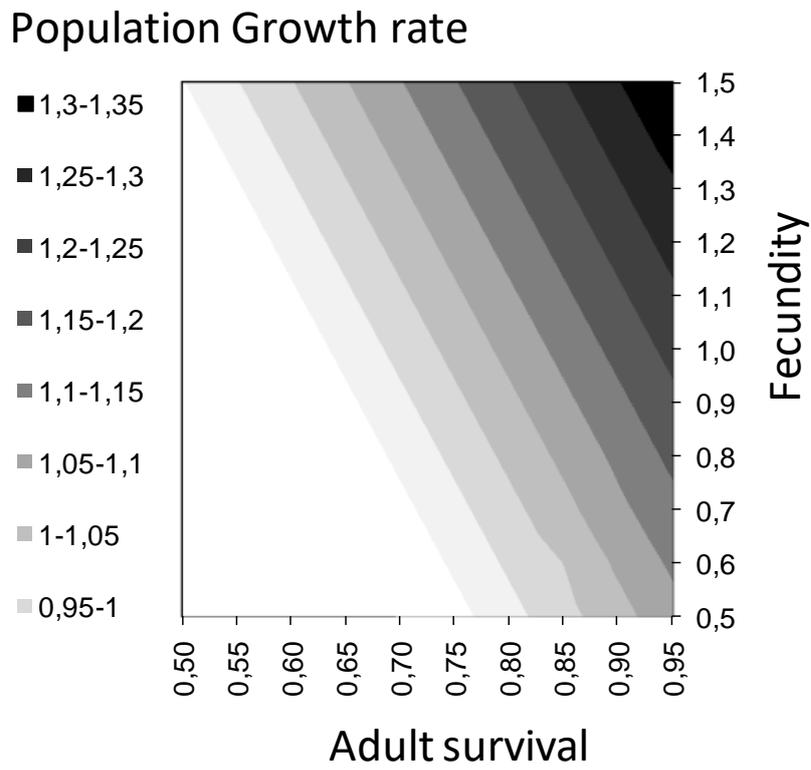


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612 **Figure 2:** Values of the deterministic growth rate ( $\lambda$ ) as a function of the adult survival and  
613 fecundity rates. Dark grey shading indicates high value of  $\lambda$ . Other demographic parameters are  
614  $\sigma=0.5$ ;  $S_0=0.53$ .

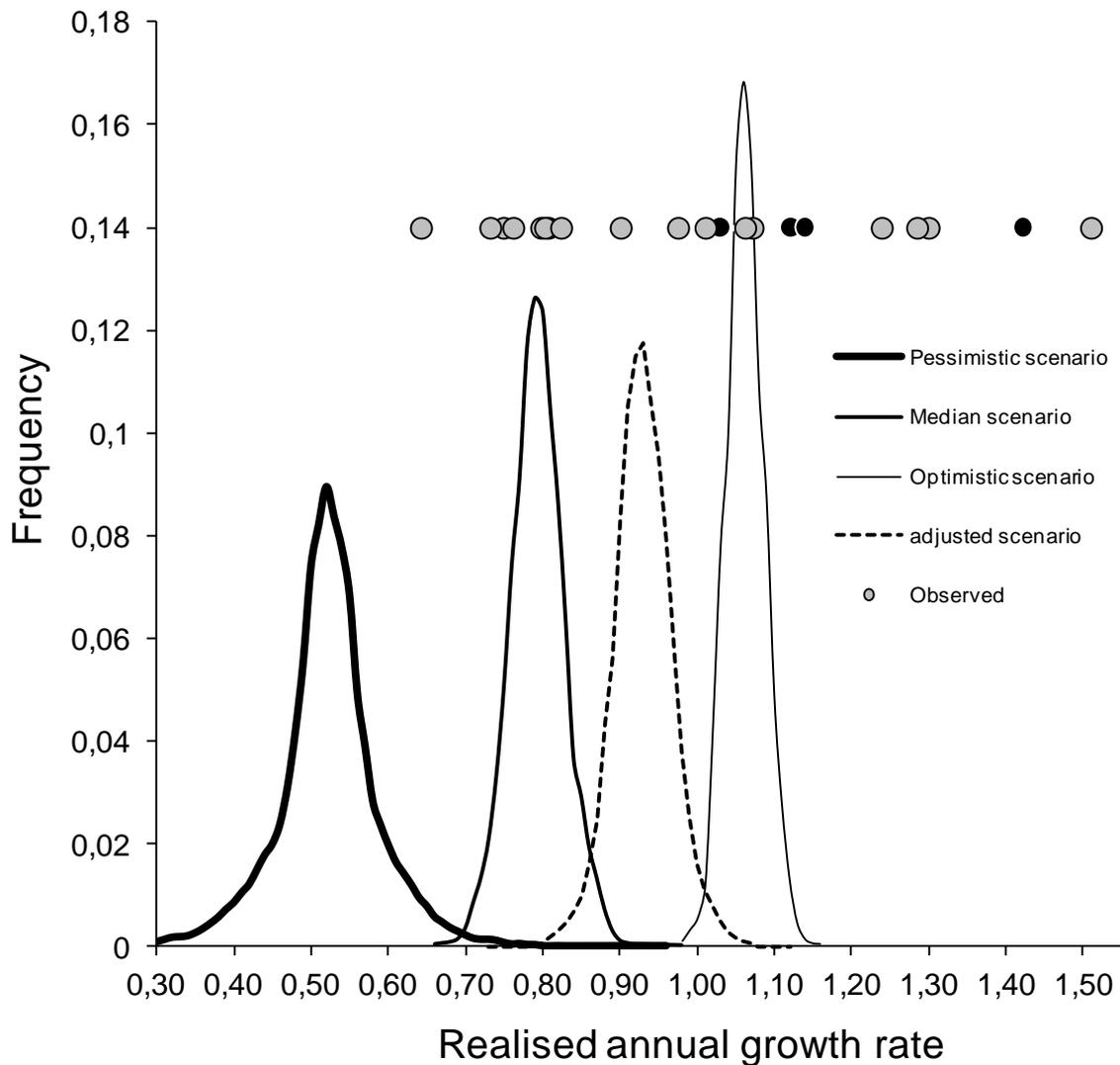
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619 **Figure 3:** Comparison between the expected and observed annual growth. Expected  
 620 distributions (lines) are based on 1000 stochastic trajectories from the stochastic individual-  
 621 based model (see the Materials and Methods for details). Observed values (circles) correspond  
 622 to the  $N_t/N_{t-1}$  ratios observed over the 1991-1995 (black circles) and 1995-2012 (grey circles)  
 623 periods. Pessimistic scenario,  $S_0=0.53$ ,  $S_{ad}=0.37$ ,  $F=0.58$ ; median scenario,  $S_0=0.53$ ,  $S_{ad}=0.59$ ,  
 624  $F=0.78$ ; Optimistic scenario,  $S_0=0.53$ ,  $S_{ad}=0.8$ ,  $F=0.99$ ; Adjusted scenario,  $S_0=0.57$ ,  $S_{ad}=0.69$ ,  
 625  $F=0.84$ .  
 626

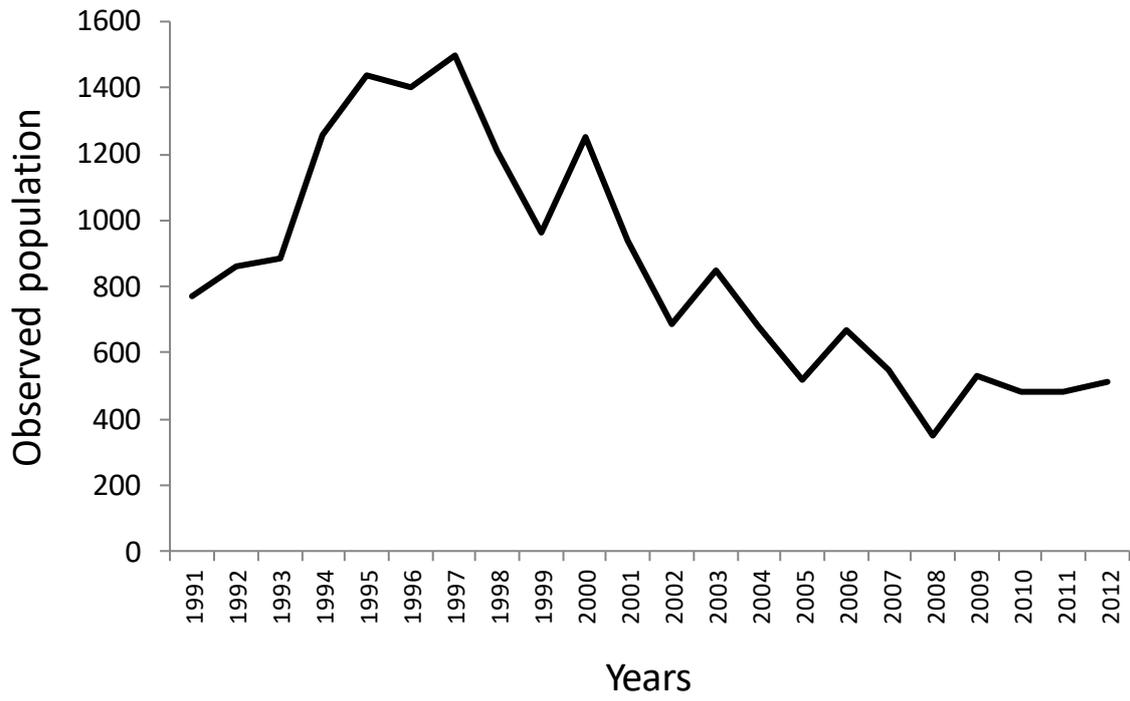


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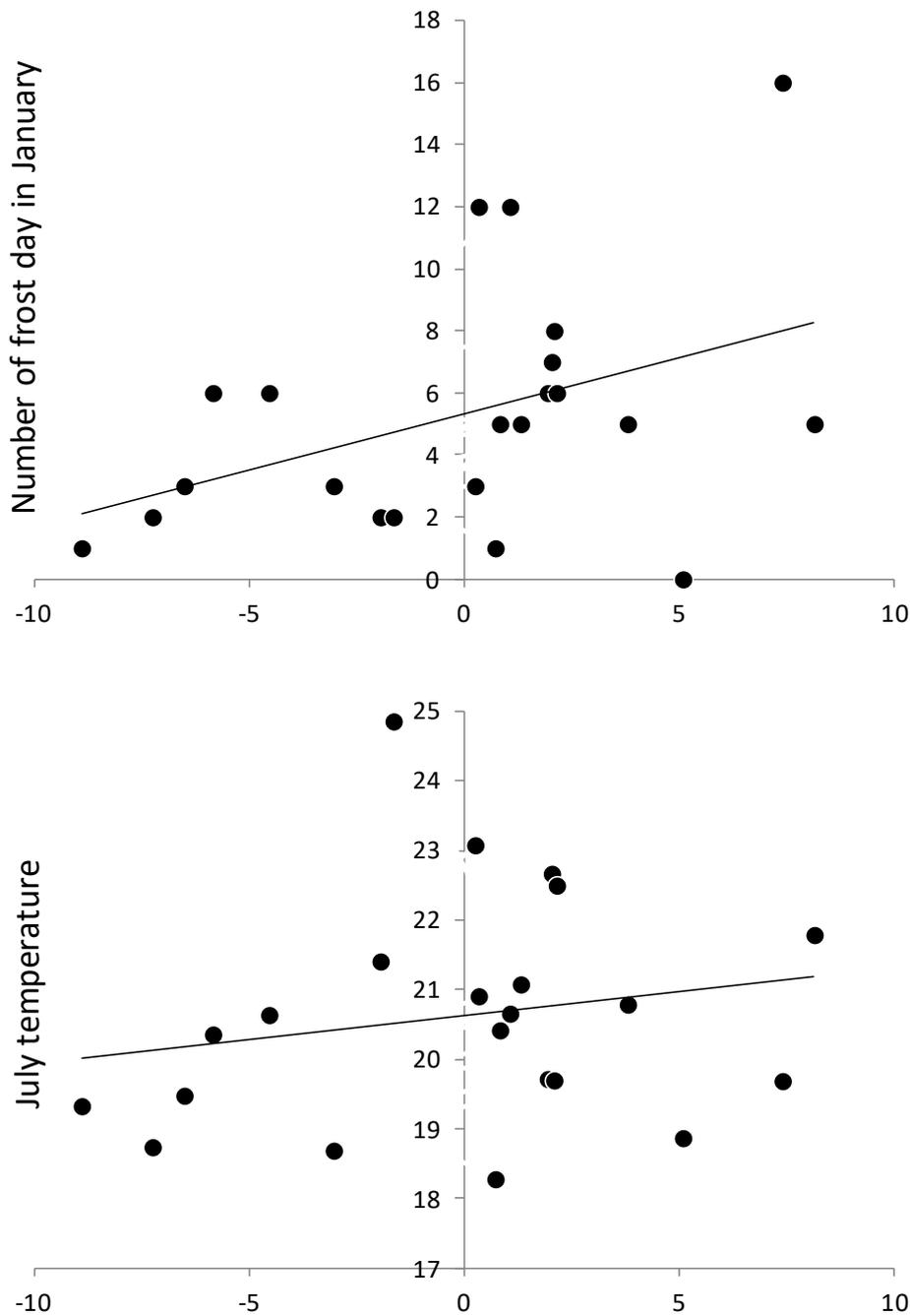
630 **Figure 4:** Change in bat abundance (as estimated from winter counts) between 1991 and 2012



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632

633 **Figure 5.** Effect of number of frost day in January (upper panel) and July temperature (lower  
634 panel) on changes in the observed population size. Values of July temperature were recorded in  
635 the year prior to the winter bat counts. Climate variables are adjusted to the year effect and  
636 railway traffic effect, so changes in the observed population size are expressed in residuals from  
637 the modelling.



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642 **Supplementary material - Appendix S1**

643 Characteristics of the hibernaculum of pipistrelle bats (*Pipistrellus pipistrellus*) located in a  
644 railway tunnel (600 meter long, Picture 1).The counting method is a direct visual count of  
645 individuals who are located in shallow notches. These notches are expansion joint vertical  
646 depth of 10 cm between concrete slabs (Picture 2), This is close to some natural cracks (Picture  
647 3) The count procedure leads thus to very thin measurements errors, because all individuals are  
648 observable.  
649



**Picture 1:** railway tunnel where the hibernaculum of pipistrelle bats is located

650



**Picture 2:** pipistrelle in a notch between concrete slabs.



**Picture 3:** pipistrelle in a natural cracks

651

652

653 **Supplementary material - Appendix S2:** Table of correlations (Spearman's rank test) between  
 654 the pairs of weather variables used in the modelling.  $T_{.day}$  is the local ambient temperature at  
 655 the time of the count;  $T_{.January}$  is the average temperature in January;  $T_{.winter}$  is the average  
 656 temperature in the winter (December-January-February);  $T_{.Anomalies}$  is the temperature anomaly  
 657 observed in January relative to the average temperatures over the 1951-1989 period;  $Frost\ day$   
 658 is the number of frost days in January;  $P_{.June}$  is the rainfall recorded in June of the previous year;  
 659  $P_{.July}$  is the rainfall recorded in July of the previous year;  $T_{.June}$  is the average temperature in June  
 660 of the previous year;  $T_{.July}$  is the average temperature in July of the previous year; Significance  
 661 tests are indicated in bold characters ( $\alpha=0.05$ ).  
 662

	Winter variables					Spring variables			
	$T_{.day}$	$T_{.January}$	$T_{.winter}$	$T_{.Anomalies}$	$Frost\ day$	$P_{.June}$	$P_{.July}$	$T_{.June}$	$T_{.July}$
<i>Year</i>	$p=0.63$ $\rho=-0.12$	$p=-0.83$ $\rho=-0.05$	$p=-0.87$ $\rho=0.04$	$p=-0.63$ $\rho=0.12$	$p=-0.45$ $\rho=-0.18$	$p=0.54$ $\rho=-0.14$	$p=0.45$ $\rho=0.18$	<b><math>P=0.004</math></b> <b><math>\rho=0.61</math></b>	$P=0.79$ $\rho=0.06$
<i>T<sub>.day</sub></i>		$p=0.11$ $\rho=0.39$	$P=0.52$ $\rho=0.16$	<b><math>p=-0.03</math></b> <b><math>\rho=0.50</math></b>	$P=0.34$ $\rho=-0.24$	$p=0.94$ $\rho=-0.02$	$p=0.15$ $\rho=0.35$	$p=0.56$ $\rho=-0.14$	$p=0.55$ $\rho=-0.14$
<i>T<sub>.January</sub></i>			<b><math>P&lt;0.001</math></b> <b><math>\rho=0.76</math></b>	<b><math>p=0.02</math></b> <b><math>\rho=0.53</math></b>	<b><math>P=0.002</math></b> <b><math>\rho=-0.67</math></b>	$p=0.37$ $\rho=0.22$	$p=0.66$ $\rho=0.11$	$p=0.85$ $\rho=-0.05$	$p=0.73$ $\rho=-0.08$
<i>T<sub>.winter</sub></i>				<b><math>P=0.01</math></b> <b><math>\rho=0.57</math></b>	<b><math>P&lt;0.001</math></b> <b><math>\rho=-0.72</math></b>	$p=0.31$ $\rho=0.25$	$p=0.23$ $\rho=0.28$	$p=0.45$ $\rho=0.18$	$p=0.78$ $\rho=-0.06$
<i>T<sub>.Anomalies</sub></i>					$P=0.28$ $\rho=-0.26$	$p=0.39$ $\rho=0.21$	$p=0.10$ $\rho=0.38$	$p=0.80$ $\rho=-0.06$	$p=0.62$ $\rho=0.12$
<i>Frost day</i>						$p=0.93$ $\rho=-0.02$	$p=0.20$ $\rho=-0.31$	$p=0.15$ $\rho=-0.34$	$p=0.47$ $\rho=0.18$
<i>P<sub>.June</sub></i>							<b><math>p=0.04</math></b> <b><math>\rho=-0.45</math></b>	$p=0.40$ $\rho=-0.19$	$p=0.84$ $\rho=-0.05$
<i>P<sub>.July</sub></i>								$p=0.82$ $\rho=0.06$	$p=0.95$ $\rho=-0.01$
<i>T<sub>.June</sub></i>									$p=0.77$ $\rho=-0.07$

663 \* Spearman's rho showed no important correlations between variables (correlation coefficient  
 664  $|\rho| < 0.5$ ; Freckleton 2002).

665

666 **Reference**

667 FRECKLETON, R.P. 2002. On the misuse of residuals in ecology: regression of residuals vs. multiple  
 668 regression. *Journal of Animal Ecology* 71: 542-545.

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676 **Supplementary Material. - Appendix S3 of The adjusted scenario.**

677 We aimed to examine an additional scenario (hereafter, adjusted scenario) as follows: (i) with  
678 the same demographic structure and properties as our median scenario (i.e., a scenario based  
679 on the most reliable demographic parameters provided by the literature) and (ii) yielding a  
680 growth rate similar to the one observed over the 1995-2010 period (0.93).

681 For this purpose, we kept the same transition matrix structure as the median scenario (see  
682 Figure S2.1 below, this model yields a deterministic growth  $\lambda_{\text{median}}=0.797$ ), and we slightly  
683 modified the demographic parameters to obtain  $\lambda_{\text{adjusted}}=0.93$ .

684 This can be achieved by multiplying the transition matrix by a constant term,  $\alpha=$   
685  $\lambda_{\text{adjusted}}/\lambda_{\text{median}}=1.17$ , or by multiplying the demographic parameters such that all of the non-  
686 zero terms of the transition matrix are multiplied by  $\alpha$  (Caswell 2001).

687  
688 **Figure S2.1.** Transition matrix corresponding to the median scenario.  $\sigma=0.5$ ;  $s_0=0.53$ ;  $s_{ad}=0.59$ ;  
689  $F=0.78$ .

690  
691 
$$\begin{pmatrix} \sigma s_0 F & \sigma s_0 F \\ s_{ad} & s_{ad} \end{pmatrix}$$
  
692  
693  
694  
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698

699 We obtained the following parameters for the adjusted scenario:

700  $s_0' = \sqrt{\alpha} \times 0.53 = 0.57$

701  $s_{ad}' = \alpha \times 0.59 = 0.69$

702  $F' = \sqrt{\alpha} \times 0.78 = 0.84$

703  
704 This new set of parameters leads to a population with similar demographic properties as the  
705 median scenario (i.e., the same generation time and proportions of age classes at demographic  
706 equilibrium) but a different deterministic growth rate ( $\lambda_{\text{adjusted}}=0.93$ ).

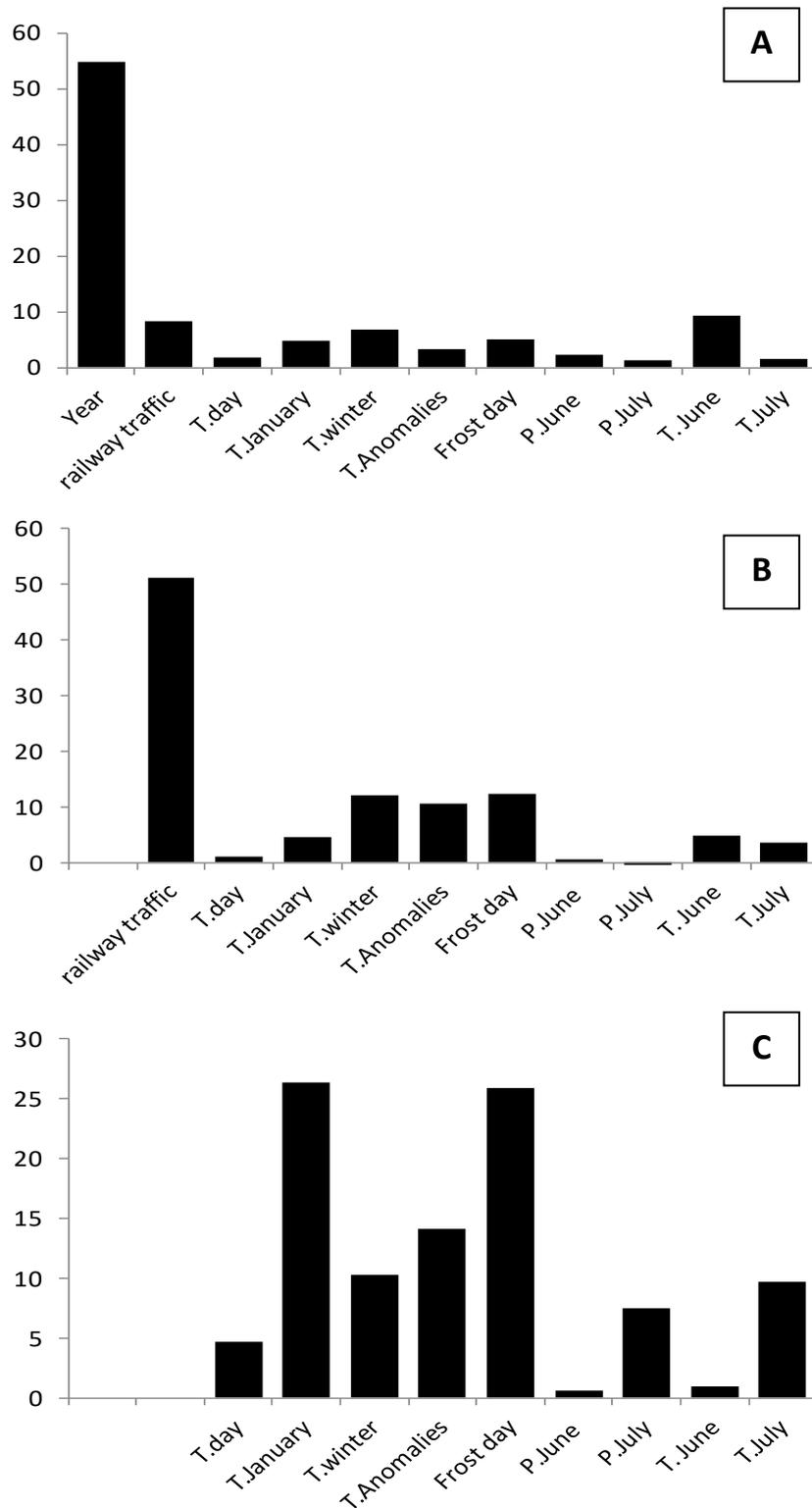
707  
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709 **Supplementary material - Appendix S4: Model selection table**

<b>Model</b>	<b>AIC</b>
Count ~ Year	1574
Count ~ Traffic	3154
Count ~ T.day	3083
Count ~ T.January	1574
Count ~ T.winter	2907
Count ~ T.Anomalies	2467
Count ~ Frost day	2922
Count ~ P.June	3130
Count ~ P.July	3155
Count ~ T. June	1574
Count ~ T.July	3153
Count ~ Year + Traffic	621
Count ~ Year + T.day	1532
Count ~ Year + T.January	1470
Count ~ Year + T.winter	1533
Count ~ Year + T.Anomalies	1529
Count ~ Year + Frost day	1454
Count ~ Year + P.June	1558
Count ~ Year + P.July	1560
Count ~ Year + T. June	1432
Count ~ Year + T.July	1564
Count ~ Year + Traffic	3090
Count ~ Traffic + T.day	3079
Count ~ Traffic + T.January	3090
Count ~ Traffic + T.winter	2909
Count ~ Traffic + T.Anomalies	2443
Count ~ Traffic + Frost day	2921
Count ~ Traffic + P.June	3128
Count ~ Traffic + P.July	3155
Count ~ Traffic + T. June	2688
Count ~ Traffic + T.July	3154
Count ~ Year + Traffic +T.day	597
Count ~ Year + Traffic +T.January	539
Count ~ Year + Traffic +T.winter	552
Count ~ Year + Traffic +T.Anomalies	553
Count ~ Year + Traffic +Frost day	467
Count ~ Year + Traffic +P.June	622
Count ~ Year + Traffic +P.July	606
Count ~ Year + Traffic +T. June	622
Count ~ Year + Traffic +T.July	603
Count ~ Year + Traffic +T.day + P.June	598
Count ~ Year + Traffic +T.day + P.July	593
Count ~ Year + Traffic +T.day + T. June	597
Count ~ Year + Traffic +T.day + T.July	577
Count ~ Year + Traffic + T.January + P.June	536
Count ~ Year + Traffic + T.January + P.July	533
Count ~ Year + Traffic + T.January + T. June	541
Count ~ Year + Traffic + T.January + T.July	516
Count ~ Year + Traffic + T.winter + P.June	553
Count ~ Year + Traffic + T.winter + P.July	539
Count ~ Year + Traffic + T.winter + T. June	553
Count ~ Year + Traffic + T.winter + T.July	517
Count ~ Year + Traffic + T.Anomalies + P.June	553
Count ~ Year + Traffic + T.Anomalies + P.July	537
Count ~ Year + Traffic + T.Anomalies + T. June	555
Count ~ Year + Traffic + T.Anomalies + T.July	524
Count ~ Year + Traffic + Frost day + P.June	469
Count ~ Year + Traffic + Frost day + P.July	465
Count ~ Year + Traffic + Frost day + T. June	467
Count ~ Year + Traffic + Frost day + T.July	<b>435</b>

711 **Supplementary material - Appendix S5:**

712 **Figure S3.1.** Identification of the most likely causal factors of temporal variations in recorded  
 713 bat abundance, using hierarchical partitioning (R package *hier.part*), including (A) All variables;  
 714 (B) variables adjusted to the yearly trend and (C) variables adjusted to both yearly trend and  
 715 railway traffic effects.  
 716



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