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.

Christian Kerbiriou, Jean François Julien, Sophie Monsarrat, Philippe Lustrat, Alexandre Haquart, Alexandre Robert

► **To cite this version:**

Christian Kerbiriou, Jean François Julien, Sophie Monsarrat, Philippe Lustrat, Alexandre Haquart, et al.. 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.. Wildlife Research, 2015, 42 (1), pp.35. 10.1071/WR14197 . hal-02554293

HAL Id: hal-02554293

<https://hal.science/hal-02554293>

Submitted on 25 Apr 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Title: 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.

Running head: Pragmatic approach to analyse count data of bats in hibernaculum

Authors:

Christian Kerbiriou¹, Jean François Julien¹, Sophie Monsarrat¹, Philippe Lustrat², Alexandre Haquart³, and Alexandre Robert¹

Authors affiliations:

¹Centre d'Ecologie et des Sciences de la Conservation- UMR 7204 MNHN-CNRS-UPMC, 55 rue Buffon, 75005 Paris, France.

²Natur Research, Fontainebleau, France

³Bd Maréchal Foch - BP58 - 34140 Mèze, France

Corresponding author:

Christian KERBIRIOU

Muséum National d'Histoire Naturelle

UMR 7204 MNHN-CNRS-UPMC, 55 rue Buffon, 75005 Paris, France

Tel. [+0033] 1 40 79 38 31 ; Fax. [+0033] 1 40 79 38 35

E-mail: kerbiriou@mnhn.fr

Words count: 5902

Abstract (Words count: 349)

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

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

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

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

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

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

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

Key words

Pipistrellus pipistrellus; Population dynamics; count monitoring; deterministic matrix model; Stochastic-individual-based population model; disturbance

Introduction

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

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

Most of the European bat populations have a poor conservation status because of various 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)

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

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

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

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

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

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

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

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

MATERIALS AND METHODS

Study area

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

Population dynamics modelling

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

Deterministic matrix model

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

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

Approximate position of figure 1

Stochastic, individual-based population model

In addition, to compare the actual observed annual growth rates with their theoretical distribution under demographic stochasticity in the absence of immigration and emigration, we developed a stochastic two-sex individual-based population model. This model allowed the complete description of all of the individuals in terms of sex and age. In each time interval (year), adult individuals were randomly paired according to a polygynous mating system with an unrestricted harem size, i.e., we assumed that all mature females present in the population can reproduce provided that there was at least one male in the population (Legendre *et al.* 1999). This hypothesis is realistic, as recent results suggest that the proportion of breeding females among adult females is usually very high (about 95%, see Barclay *et al.*, 2004). The reproductive success of each pair was determined according to a Bernoulli drawing of parameter F (in cases where $F < 1.0$), or a Poisson trial of parameter F (in cases where $F \geq 1$). The sex of each newborn individual was randomly determined according to a 1:1 mean sex ratio. Reproduction was followed by the differential mortality of individuals according to age-specific annual survival rates (s_0 and s_{ad}). Each individual survival event was drawn from a Bernoulli

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

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

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

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

Statistical analysis

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

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

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

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

RESULTS

Comparison of observed growth rates and those assessed with modelling.

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

Approximate position of figure 2

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

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

Approximate position of figure 3

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

Approximate position of figure 4

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

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

Population trend analyses and the importance of weather on between year variations.

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

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

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

Approximate position of figure 5

DISCUSSION

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

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

Demographic processes underlying the observed local dynamics

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

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

Population trends and environmental effects

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

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

Limitations and perspectives

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

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

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

Recommendations

To conduct a meaningful analysis of time-series count data of bat in hiber culatum, it is necessary

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

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

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

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

Acknowledgements

The manuscript was edited for language use, grammar, punctuation, spelling and overall style by American Journal Experts. We are grateful to two anonymous reviewers for their constructive comments.

Reference

- Anonym, (1995) Biodiversity: Report of the UK steering group, London.
- Arlettaz R., Christe, P., Lugon, A., Perrin, N., and Vogel, P. (2001). Food availability dictates the timing of parturition in insectivorous mouse-eared bats. *Oikos* **95**, 105–111.
- Arthur, L., and Lemaire, M. (2009). Les chauves-souris de France, Belgique, Luxembourg et Suisse. Biotope, Mèze, Muséum National d'Histoire Naturelle, Paris.
- Balmford, A., Crane, P., Dobson, A., Green, R. E., and Mace, G. M. (2005). The 2010 challenge: data availability, information needs and extraterrestrial insights. *Philosophical Transaction of the Royal Society Biology* **360**, 221–228.
- Barclay, R. M. R., Ulmer, J., MacKenzie, C. J. A., Thompson, M. S., Olson, L., McCool, J., Cropley, E., and Poll, G. (2004). Variation in the reproductive rate of bats. *Canadian Journal of Zoology* **82**, 688-693.
- Bat conservation Trust Available at <http://www.bats.org.uk> [verified September 2014].
- Beissinger, S. R., and McCullough, D.R. (2002). Population viability analysis. Chigago Press, Chigago.
- Blehert, D. S., Hicks, A.C., Behr, M., Meteyer, C. U., Berlowski-Zier, B. M., Buckles, E.L., Coleman, J. T. H., Darling, S. R., Gargas, A., Nivers, R., Okoniewski, J.C., Rudd, R. J., and Stone, W. B. (2009). Bat White-Nose Syndrome: An Emerging Fungal Pathogen? *Science* **323**, 227.

474 Butchart, S. H. M., Stattersfield, A. J., Baillie, J., Bennun, L. A., Stuart, S. N., Akçakaya, H. R.,
 475 Hilton-Taylor, C., and Mace, G. M. (2005). Using Red List Indices to measure progress
 476 towards the 2010 target and beyond. *Philosophical Transaction of the Royal Society*
 477 *Biology* **360**, 255–268.

478 Caswell, H. (2001). Matrix population models. Construction, analysis and interpretation.
 479 Sinauer, Sunderland.

480 Crawley, M. J. (2009). The R book. John Wiley and Sonc. Chicago.

481 Dietz, C., Dietz, I., Ivanova, T. and Siemers, B.M. (2006). Effects of forearm bands on horseshoe
 482 bats (Chiroptera: Rhinolophidae). *Acta Chiropterologica* **8**, 523-535.

483 Dietz, C., von Helversen, O., and Nill, D. (2007). Handbuch der Fledermäuse Europas. Franckh-
 484 Kosmos-Naturführer Verlargs, Stuttgart.

485 Eurobat Available at <http://www.eurobat.org> [verified 30 September 2014].

486 European Environment Agency (2013). European bat population trends – A prototype
 487 biodiversity indicator. Technical report No 19/2013 Available at
 488 <http://www.eea.europa.eu/publications/european-bat-population-trends-2013> [verified
 489 September 2014].

490 European Climate Assemmment Dataset. Available from: <http://eca.knmi.nl> [verified September
 491 2014]

492 Faraway, J.J. (2006). Extending the linear model with R, Generalized linear, miwed effects and
 493 nonparametric regression models. Chapman and Hall/CRC. Boca Raton 301p.

494 Ferrière, R., Sarrazin, F., Legendre, S., and Baron, J-P. (1996). Matrix population models applied
 495 to viability analysis and conservation: Theory and practice using the ULM software. *Acta*
 496 *Oecologica* **17**, 629-656.

497 Frick, W. F., Pollock, J. F., Hicks, A. C., Langwig, K. E., Reynolds, D. S., Turner, G. G., Butchkoski,
 498 C. M., and Kunz, T.H. (2010). An Emerging Disease Causes Regional Population Collapse of
 499 a Common North American Bat Species. *Science* **329(5992)**, 679-682.

500 Gaisler, H., Hanak, V., and Horacek, I. (1981). Remarks on the current status of bats populations
 501 in Czechoslovakia. *Myotis* **18**, 68-75.

502 Gerell, R., and Lunddberg, K. (1990). Sexual differences in survival rates of adult pipistrelle bats
 503 (*Pipistrellus pipistrellus*) in South Sweden. *Oecologia* **83**, 401-404.

504 Gore J. A., Lazure, L., and Ludlow, M. E. (2012). Decline in the Winter Population of Gray Bats
 505 (*Myotis grisescens*) in Florida. *Southeastern Naturalist* **11**, 89-98.

506 Grindal, S. D., Collard T. S., Brigham, M., and Barclay, R.M.R. (1992). The Influence of
 507 Precipitation on Reproduction by Myotis Bats in British Columbia. *American Midland*
 508 *Naturalist* **128**, 339-344.

509 IAU, (2011). Base de connaissance sur le Mode d'occupation du sol (Mos)
 510 Available at <http://www.iaurif.org/> [verified 30 September 2014].

511 Infoclimat, Available at: <http://www.infoclimat.fr/archives> [verified September 2014].

512 Kurta, A., and Teramino, J. A. (1992). Bat Community Structure in an Urban Park. *Ecography* **15**,
 513 259-261.

514 Legendre, S., and Clobert, J. (1995). ULM, a software for conservation and evolutionary
 515 biologists. *Journal of Applied Statistics* **22**, 817-834.

516 Legendre, S., Clobert, J., Møller, A. P., and Sorci, G. (1999). Demographic stochasticity and social
 517 mating system in the process of extinction of small populations: the case of passerines
 518 introduced to New Zealand. *American Naturalist* **153**, 449-463.

519 Loeb, S. C., Christopher, J. P., and Hall, S. T. (2009). Relationship between urbanization and bat
 520 community structure in national parks of the southeastern U.S. *Urban Ecosystems* **12**,
 521 197-214.

522 Lustrat, P., and Julien, J.F. (1993). Un important gîte d'hibernation de chauves-souris à Paris
 523 (France). *Mammalia* **57**, 447-448.

524 Mac Cracken, G. F. (1989). Cave conservation: special problems of bats. *Bulletin of the National*
 525 *Speleological Society* **51**, 49–51.

526 Mac Nally, R. (2000). Regression and model building in conservation biology, biogeography and
 527 ecology: the distinction between and reconciliation of 'predictive' and 'explanatory'
 528 models. *Biodiversity and Conservation* **9**, 655–671

529 MEA, (2005). Available at <http://www.maweb.org/en/index.aspx> [verified September 2014].

530 Mitchell-Jones, A. J., Bihari, Z., Masing, M., and Rodrigues, L. (2007) Protecting and managing
 531 underground sites for bats. EUROBATS Publication Series No. 2 (English version). (UNEP /
 532 EUROBATS Secretariat: Bonn)

533 Mumford, R. E. (1958). Population Turnover in Wintering Bats in Indiana. *Journal of*
 534 *Mammalogy* **39**, 253-261.

535 O'Donnell, C. F. J. (2000). Conservation status and causes of decline of the threatened New
 536 Zealand long-tailed bat *Chalinolobus tuberculatus* (Chiroptera: Vespertilionidae). *Mammal*
 537 *Review* **30**, 89–106.

538 O'Shea, T. J., Bogan, M. A., and Ellison, L.E. (2003). Monitoring trends in bat populations of the
 539 United States and territories: status of the science and recommendations for the future.
 540 *Wildlife Society Bulletin* **31**, 16-29.

541 Prendergast, J. A., Jensen, W. E., and Roth, S. D. (2010). Trends in abundance of hibernating
 542 bats in a karst region of the southern great plains. *The Southwestern Naturalist* **55**, 331-
 543 339
 544 Punt, A. (1970). Round table discussion on bat conservation proceeding of the Second
 545 International Bat Research Conference 3-4.
 546 Sandel, J. K., Benatar, G. R., Burke, K. M., Walker, C. W., Lacher, T. E., and Honeycutt, R.L.
 547 (2001). Use and selection of winter hibernacula by the eastern pipistrelle (*Pipistrellus*
 548 *subflavus*) in Texas. *Journal of Mammalogy* **82**, 173-178.
 549 Saraux, C., Le Bohec C., Durant, J. M., Viblanc, V. A., Gauthier-Clerc, M., Beaune, D., Park, Y. J.,
 550 Yoccoz, N. G., Stenseth, N. C., and Le Maho, Y. (2011). Reliability of flipper-banded
 551 penguins as indicators of climate change. *Nature* **471**, 254-254.
 552 Schober, W., and Grimmberger, E. (1998). Die Fledermäuse Europas. (Kosmos-Naturführer:
 553 Stuttgart)
 554 Sendor, T., and Simon, M. (2003). Population dynamics of the pipistrelle bat: effects of sex, age
 555 and winter weather on seasonal survival. *Journal of Animal Ecology* **72**, 308-320.
 556 Simon, M., Hüttenbügel, S., and Smit-Viergutz, J. (2004). Ecology and conservation of bats in
 557 villages and town. (Bundesamt für Naturschutz – Federal Agency for Nature Conservation:
 558 Gdansk).
 559 Speakman, J. R., Webb P. I., and Racey, P. A. (1991). Effects of Disturbance on the Energy
 560 Expenditure of Hibernating Bats. *Journal of Applied Ecology* **28**, 1087-1104.
 561 Stebbing, R. E. (1988). Conservation of European bats. Christopher Helm. London.
 562 Swanepoel, R. E., Racey, P. A., Shore, R. F., and Speakman, J. R. (1999) Energetic effects of
 563 sublethal exposure to lindane on pipistrelle bats (*Pipistrellus pipistrellus*) *Environmental*
 564 *Pollution* **104**, 169-177.

565 Thompson, M. J. A. (1987). Longevity and survival of female pipistrelle bat (*Pipistrellus*
 566 *pipistrellus*) on the Vale of York, England. *Journal of Zoology* **211**, 209-214.

567 Thomas, D. W., and Laval, R. K. (1988). Survey and census methods. 77-89pp *In* T. H. Kunz.
 568 editor. Ecological and behavioral method; for the study of bats. Smithsonian Institution
 569 Press. Washington, D.C. USA.

570 Trombulak, S. C., Higuera, F. E., and Des Meules, M. (2001) Population trends of wintering bats
 571 in vermont. *Northeastern Naturalist* **8(1)**, 51-62.

572 Tuttle, M. D. (1976). Population Ecology of the Gray Bat (*Myotis Grisescens*): Factors Influencing
 573 Growth and Survival of Newly Volant Young. *Ecology* **57**, 587-595.

574 Tuttle, M. D. (2003). Estimating population sizes of hibernating bats in caves and mines. *In*
 575 O'Shea and Bogan (Eds.). Monitoring trends in bat populations of the United States and
 576 Territories: problems and prospects. Information and Technology Report USGS/BRD/TR.
 577 2003.

578 Walsh, A. L., and Harris, S. (1996). Foraging habitat preference of vespertilionid bats in Britain.
 579 *Journal of Applied Ecology* **33**, 508-518.

580 Warren, R. D., and Witter, M. S. (2002). Monitoring trends in bat populations through roost
 581 surveys: methods and data from *Rhinolophus hipposideros*. *Biological Conservation* **105**,
 582 255–261.

583 Webb, P. I., Speakman, J. R., and Racey, P.A. (1996). Population dynamics of a maternity colony
 584 of the pipistrelle bat (*Pipistrellus pipistrellus*) in north-east Scotland. *Journal of Zoology*
 585 **240**, 777-780.

586 Wickramasinghe, L. P., Harris, S., Jones, G., and Vaughan, N. (2003). Bat activity and species
 587 richness on organic and conventional farms: impact of agricultural intensification. *Journal*
 588 *of Applied Ecology* **40**, 984-993.

589 Zahn, A. (1999). Reproductive success, colony size and roost temperature in attic-dwelling bat
590 *Myotis myotis*. *Journal of Zoology* **247**, 275–280.
591

Table 1: Effects of disturbance and meteorological variables on the estimates of number of bat.

T_{.day} is the local ambient temperature at the time of the count; T_{.January} is the average temperature in January; T_{.winter} is the average temperature in winter (December-January-February); T_{.Anomalies} is the temperature anomaly observed in January relative to the average temperatures over the 1951-1989 period; *Frost day* is the number of frost days in January; P_{.June} is the rainfall recorded in June of the previous year; P_{.July} is the rainfall recorded in July of the previous year; T_{.June} is the average temperature in June of the previous year; T_{.July} is the average temperature in July of the previous year; Slope of the effect (β) are given for significant test.

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

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

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

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

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

631

632

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

Supplementary material - Appendix S1

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

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

Picture 2: pipistrelle in a notch between concrete slabs.

Picture 3: pipistrelle in a natural cracks

Supplementary material - Appendix S2: Table of correlations (Spearman's rank test) between the pairs of weather variables used in the modelling. *T.day* is the local ambient temperature at the time of the count; *T.January* is the average temperature in January; *T.winter* is the average temperature in the winter (December-January-February); *T.Anomalies* is the temperature anomaly observed in January relative to the average temperatures over the 1951-1989 period; *Frost day* is the number of frost days in January; *P.June* is the rainfall recorded in June of the previous year; *P.July* is the rainfall recorded in July of the previous year; *T.June* is the average temperature in June of the previous year; *T.July* is the average temperature in July of the previous year; Significance tests are indicated in bold characters ($\alpha=0.05$).

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

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

Reference

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

Supplementary Material. - Appendix S3 of The adjusted scenario.

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

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

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

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

$$\begin{pmatrix} \sigma s_0 F & \sigma s_0 F \\ s_{\text{ad}} & s_{\text{ad}} \end{pmatrix}$$

We obtained the following parameters for the adjusted scenario:

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

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

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

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

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

Model	AIC
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	435

Supplementary material - Appendix S5:

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