

Information on population trends and biological constraints from bat counts in roost cavities: a 22-year case study of a pipistrelle bats (*Pipistrellus pipistrellus* Schreber) hibernaculum

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Abstract

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 1993–94, 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⁻¹), 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 behaviour and reproduction success, respectively.

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

Additional keywords: count monitoring, deterministic matrix model, disturbance, population dynamics, stochastic individual-based population model.

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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 2013). 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 studies of animal population dynamics 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 Fenton 2003), agricultural intensification (Swanepoel *et al.* 1999; Wickramasinghe *et al.* 2003), urbanisation (Kurta and Teramino 1992; Loeb *et al.* 2009) and forest management (O'Donnell 2000). Human activities strongly reduce the availability of underground sites used by bats for breeding or/and hibernation. Whereas some underground sites are filled in, blocked up or transformed (Mitchell-Jones *et al.* 2007), others are opened for tourism activities, resulting in recurrent disturbances. Such activities may have major consequences on the population dynamics of bat species at large scales because (1) several studies have stressed the high sensitivity of bats to human disturbance (Mac Cracken 1989; Speakman *et al.* 1991; Gore *et al.* 2012); and (2) in some cases, the loss of a single site can affect the dynamics of bat populations over areas of several thousands of square kilometres (Mitchell-Jones *et al.* 2007). Within this context, an increasing number of bat populations occurring in roost cavities are protected and regularly counted (see the Bat Conservation Trust (<http://www.bats.org.uk>, verified September 2014) and Eurobats annual reports (Available at <http://www.eurobat.org>, verified 30 September 2014). However, because of the managers' perception that hibernacula counts exhibit chaotic variations over time, only few hibernacula counts are regularly analysed, which, in turn may lead to the abandonment of such monitoring. Nevertheless, efforts have been made to analyse count data provided by volunteers in the context of breeding-roost surveys and to provide sound assessment of population trends (Warren and Witter 2002). Less effort has been devoted so far to hibernaculum monitoring, despite the availability of hibernaculum count data and the need for conservationists to detect population declines when formulating management decisions (Trombulak *et al.* 2001; Frick *et al.* 2010). O'Shea *et al.* (2003) advocated that new techniques must be explored and modern statistical designs applied so as to improve the scientific basis for conclusions about future bat-population trends. Some recent studies and reports have considered hibernaculum count data to assess population variations (see 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 e.g. fitting a grille across the hibernaculum entrance, permitting the free passage of bats but not people, provision of additional roosting places).

The purpose of the present 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 size (for sedentary species), we hypothesise 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.* 2001), which is in turn related to reproductive success and survival of newly volant young (Tuttle 1976). Therefore, during the reproductive period, conditions of local bad weather such as low temperature or important rainfall should affect the reproductive success and then have a negative impact on population size in winter, and, subsequently, count data. However, if population dynamics are assessed only 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 behaviour linked with winter condition (Mumford 1958; Sandel *et al.* 2001) and (3) human disturbance.

Local population dynamics do not rely only 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 or emigration is not possible with count data, on the basis of 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 or immigration. In a second step, we compared this expected distribution (which depends only 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) Favourable meteorological conditions such as higher temperatures during the reproductive period should positively influence counts from roost in the following winter (larger number of young produced), whereas unfavourable 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), owing to aggregative behaviour. (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 focussed 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 that are located in shallow notches. These notches are expansion-joint vertical depth of 10 cm between concrete slabs (see Fig. S1, available as Supplementary material for this paper). Thus, the count procedure leads to very small measurement errors, because all individuals are observable. This hibernaculum is one of the most important for the species in France and the only currently known wintering site inside the city of Paris (Lustrat and Julien 1993). Although it is possible that other unknown hibernacula 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 hibernacula 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 strategy (i.e. produce a relatively low number of offspring over a longer span of time, and have high parental investment, Barclay *et al.* 2004); thus, one can expect small growth-rate variations, and this modelling

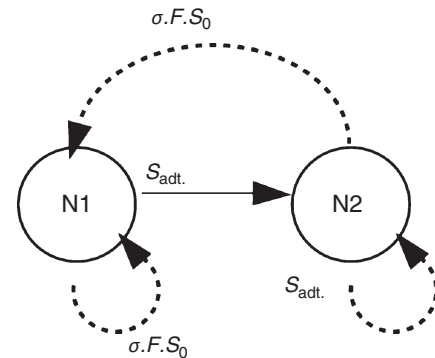


Fig. 1. Life cycle of the common pipistrelle (*Pipistrellus pipistrellus*) modelled with Leslie's matrix, where N_i is the number of individuals of Age i , σ is the sex ratio, F is the female fecundity (number of young emancipated per female), S_0 is the first-year survival probability and S_{ad} is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

approach aims to assess a range of realistic values for annual growth rates.

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, because recent results suggest that the proportion of breeding females among adult females is usually very high (~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 Lundberg 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 the population size at Time t (N_t): population size at Time $t - 1$ (N_{t-1}) were then compared with 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 as a result of 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 (1) by testing for a (decreasing or increasing) trend in numbers over the study period (1991–2012), (2) by testing for an effect of the railway traffic on bat numbers (the railway tunnel was in service until 1993); because traffic can substantially affect roost attractiveness, we included this factor in our statistical analysis as a binary variable (presence or absence of railway traffic); and finally, (3) 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, 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 the following two websites: Infoclimat (available at <http://www.infoclimat.fr/archives>, verified September 2014) and European Climate Assessment and Dataset (available at <http://eca.knmi.nl>, verified September 2014).

Statistical analysis

Because 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 Fig. S1), with the aim of avoiding the inclusion of correlated explanatory variables in statistical analyses. Weather variables in winter indeed showed strong correlations among them, as did the group of variables recorded in spring before the winter counts (Table S2, available as Supplementary material for this paper). Only the variable *average temperature in June* showed a significant yearly increasing trend (Table 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, so as 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 the yearly trend by using a sequential ANOVA (Type I) in which the effects are tested sequentially.

When the variables exhibited a significant influence, we chose 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 (for details, see Table S4, available as Supplementary material for this paper) to test whether the full model was the most parsimonious choice. We used generalised linear models (GLMs) with Poisson error distribution because of 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 Fig. S5, available as Supplementary material for this paper), 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).

The stochastic model allowed us to obtain a distribution of annual growth rates that accounted for the random fluctuations in the population size owing to demographic stochasticity under the three demographically reasonable scenarios for the pipistrelle (Fig. 3) These three contrasted scenarios were as follows: a pessimistic scenario, with $S_0=0.53$, $S_{ad}=0.37$, $F=0.58$; a median scenario, with $S_0=0.53$, $S_{ad}=0.59$, $F=0.78$; and an optimistic scenario, with $S_0=0.53$, $S_{ad}=0.8$, $F=0.99$. The 95% confidence intervals of the annual growth rates were

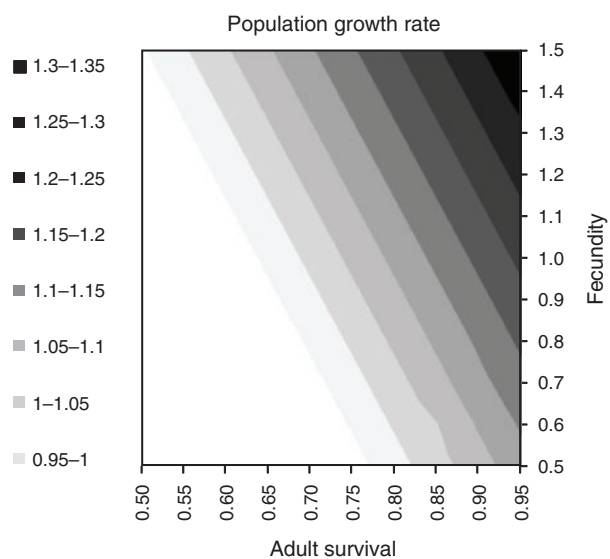


Fig. 2. Values of the deterministic growth rate (λ) as a function of the adult survival and fecundity rates. Dark grey shading indicates high value of λ . Other demographic parameters are $\sigma=0.5$, $S_0=0.53$.

(0.38–0.66), (0.72–0.86), (1.01–1.11), respectively, for the pessimistic, median and optimistic scenarios.

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

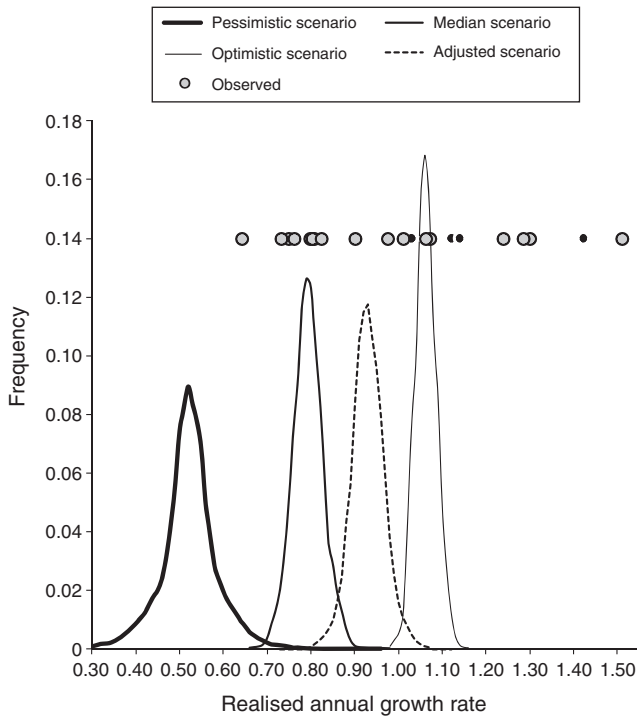


Fig. 3. Comparison between the expected and observed annual growth. Expected distributions (lines) are based on 1000 stochastic trajectories from the stochastic individual-based model (see the Materials and methods for details). Observed values (circles) correspond to the $N_t : N_{t-1}$ ratios observed over the 1991–95 (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: $S_0=0.57$, $S_{ad}=0.69$, $F=0.84$.

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 2 years (1993–94 and 2008–09, Fig. 4) in which the population size increased by >40%, presumably because of a massive immigration (see 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. Because this change is very likely to be related to an arrival of individuals following the increased attractiveness of the site, we considered only the 1995–2012 period in our subsequent analysis.

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 Fig. 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) indicated that only three of the observed growth rates were included in the confidence interval of this adjusted scenario, whereas eight were lower, and 10 were higher.

Population-trend analyses and the importance of weather on among-year variations

Over the 1991–2012 period, we did not detect any temporal autocorrelation between the year-to-year growth rates for Years t and $t+1$ (Spearman’s rank correlation test, $P=0.18$); this indicated 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

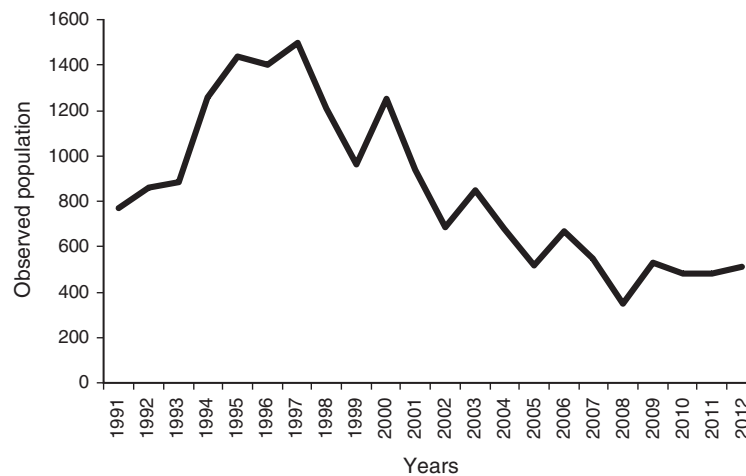


Fig. 4. Change in bat abundance (as estimated from winter counts) between 1991 and 2012.

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

T_{day} , the local ambient temperature at the time of the count; T_{January} , the average temperature in January; T_{winter} , the average temperature in winter (December–January–February); $T_{\text{Anomalies}}$, the temperature anomaly observed in January relative to the average temperatures over the 1951–89 period; Frost day, the number of frost days in January; P_{June} , the rainfall recorded in June of the previous year; P_{July} , the rainfall recorded in July of the previous year; T_{June} , the average temperature in June of the previous year; T_{July} , the average temperature in July of the previous year. Slope of the effect (β) is given for significant test

Parameter	Year		Traffic railway		Winter variable		Summer variable				
	Z	P	T_{January}	T_{day}	T_{winter}	$T_{\text{Anomalies}}$	Frost day	P_{June}	P_{July}	T_{June}	T_{July}
Effect of each variable	$Z = -4.753$	$Z = -0.085$	$Z = -0.68$	$Z = 0.34$	$Z = 0.73$	$Z = 0.06$	$Z = 0.66$	$Z = 0.41$	$Z = -0.04$	$Z = -1.39$	$Z = 0.09$
	$\beta = -0.046$	$P = 0.93$	$P = 0.50$	$P = 0.74$	$P = 0.47$	$P = 0.54$	$P = 0.51$	$P = 0.69$	$P = 0.97$	$P = 0.16$	$P = 0.92$
Effect of each variable after adjustment to the year effect	$AIC = 1574$	$AIC = 3154$	$AIC = 1574$	$AIC = 3083$	$AIC = 2907$	$AIC = 2467$	$AIC = 2922$	$AIC = 3130$	$AIC = 3155$	$AIC = 1574$	$AIC = 3153$
	$F_{1,19} = 955.63$	$F_{1,19} = 36.11$	$F_{1,19} = 106.01$	$F_{1,18} = 36.11$	$F_{1,19} = 35.18$	$F_{1,16} = 5.95$	$F_{1,18} = 113.81$	$F_{1,19} = 16.01$	$F_{1,19} = 16.01$	$F_{1,19} = 144.32$	$F_{1,19} = 12.19$
Effect of each variable after adjustment to the year effect and railway traffic	$P < 0.001$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P = 0.015$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P = 0.001$
	$\beta = -0.754$	$\beta = -0.043$	$\beta = -0.043$	$\beta = -0.009$	$\beta = -0.037$	$\beta = -0.037$	$\beta = 0.021$	$\beta = -0.001$	$\beta = -0.001$	$\beta = -0.001$	$\beta = 0.017$
	$AIC = 621$	$AIC = 1532$	$AIC = 1470$	$AIC = 1532$	$AIC = 1533$	$AIC = 1529$	$AIC = 1454$	$AIC = 1558$	$AIC = 1560$	$AIC = 1432$	$AIC = 1564$
		$F_{1,17} = 15.65$	$F_{1,18} = 83.35$	$F_{1,17} = 15.65$	$F_{1,17} = 31.96$	$F_{1,15} = 1.482$	$F_{1,17} = 116.82$	$F_{1,18} = 0.05$	$F_{1,18} = 16.56$	$F_{1,18} = 0.07$	$F_{1,18} = 19.63$
		$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P = 0.22$	$P < 0.0001$	$P = 0.82$	$P < 0.0001$	$P = 0.79$	$P < 0.0001$
		$\beta = -0.006$	$\beta = -0.038$	$\beta = -0.037$	$\beta = -0.037$	$\beta = 0.020$	$\beta = 0.020$	$\beta = -0.001$	$\beta = -0.001$	$\beta = -0.001$	$\beta = 0.019$
		$AIC = 597$	$AIC = 539$	$AIC = 552$	$AIC = 553$	$AIC = 467$	$AIC = 622$	$AIC = 606$	$AIC = 606$	$AIC = 622$	$AIC = 603$

model explained 53% of the deviance). When the weather variables were adjusted to the year trend, most of their P -values decreased drastically (sequential ANOVA, Table 1). According to AIC values (Table 1) and the percentage of independent variance explained provided by the hierarchical partitioning (see Fig. S5, available as Supplementary material for this paper), the most important variable appeared to be the yearly trend, followed by the 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 days 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 Table 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-parameterisation); 68% of this explained variance was explained by the year trend, 28% by the railway traffic presence or absence, 3% by number of frost days 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 Fig. S5). The number of common pipistrelle bats in the hibernaculum significantly declined over the period considered, i.e. 1991–2012 (Table 1, $F_{1,19} = 1416.85$; $P < 0.001$; $\beta = -0.078$ (s.e. 0.006)), which corresponds to a drastic trend of population decline, namely, 7% per year. In addition, we detected a significant negative effect of the railway traffic ($F_{1,18} = 985.84$; $P < 0.001$; $\beta = -0.781$ (s.e. 0.100)), a positive effect of number of frost days in January ($F_{1,17} = 116.82$; $P < 0.001$; $\beta = 0.021$ (s.e. 0.007); Fig. 5) and positive effect of temperature recorded in July the year before the winter bat counts, $F_{1,16} = 34.02$; $P < 0.001$; $\beta = 0.027$ (s.e. 0.018); Fig. 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 manager perception that population sizes show chaotic variations over time, we showed 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 realistic boundaries of local population variations owing to intrinsic dynamics. Despite an

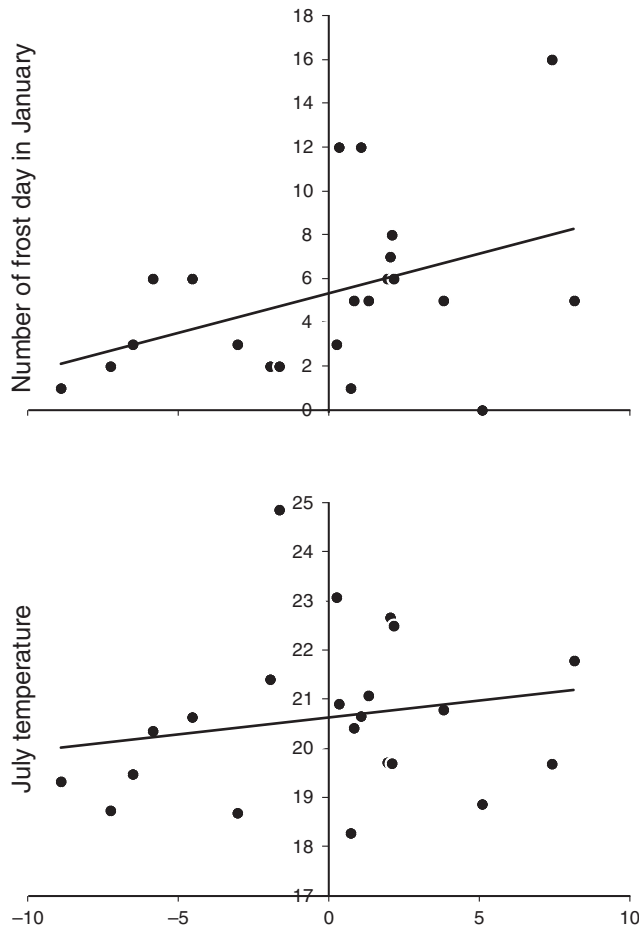


Fig. 5. Effect of number of frost days in January (upper panel) and July temperature (lower panel) on changes in the observed population size. Values of July temperature were recorded in the year before the winter bat counts. Climate variables are adjusted to the year effect and railway-traffic effect,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

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 because of demographic stochasticity, our results suggested that some of the strong year-to-year increases in the population size could not have resulted merely from intrinsic dynamics (see Figs 2, 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 1993–94 period) was 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 (MacCracken 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 behaviour 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) suggested 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 ($7\% \text{ year}^{-1}$) over the 1991–2012 period, we detected a negative effect of the railway traffic on the number of common pipistrelles and we further revealed some effects of the winter and summer temperatures. However, according to the model selection (see Table S4) and estimate and P-value (Table 1), the influence of meteorological variable is very small compared with 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 observations during the winter could, therefore, provide 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 to be linked with reproductive parameters (i.e. fledging success or/and the survival of young). This observation fit well with the pipistrelle's life cycle; July is a crucial period because it corresponds to fledging of young pipistrelle individuals 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 explained only 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 behaviours 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 not so easily detected. The hibernaculum studied here is an ideal case because available slots are standardised (joints between concrete slabs), which allows detecting almost all individuals.

We did not consider immigration–emigration in our population-dynamics models, because we had no means of adding 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 population 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 bats in hiberaculum, it is necessary

- (i) to include the local knowledge of the people involved in the field surveys in the analyses, such as, 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 to be associated with aggregation behaviour (e.g. the number of frost days in January, the average temperature in January), although they do not necessarily imply demographic consequences; and
- (iii) to include the spring–summer weather information collected during the season before the winter counts (e.g. the July rainfall), because such data are expected to affect reproductive parameters, which might, in turn, influence population dynamics.
- (iv) Our analysis also strongly suggested 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.

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