Population dynamics of Dutch bats relevant to wind energy

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POPULATION DYNAMICS OF DUTCH BATS RELEVANT TO WIND ENERGY

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Natuurinclusieve energietransitie wind en hoogspanning op land project 6: populatiedynamiek vleermuizen

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POPULATION DYNAMICS OF DUTCH BATS RELEVANT TO WIND ENERGY

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CONTENTS

SUMMARY

Bats in the Netherlands are protected by (inter)national laws, but their populations are increasingly threatened by the energy transition. The construction of, and for a number of species particularly the operation of wind turbines results in a serious pressure. Turbines can harm bats by disrupting roosts, foraging sites, and commuting routes, and causing mortality from collisions with turbine blades. Understanding the impact of this additional mortality on bat populations is critical, as bats are especially vulnerable due to their low reproduction rates. Even small increases in mortality could have significant effects on population growth, but the impact likely varies between species.

This study focusses on the question:

Does an additional mortality rate of, 1%, 5% or 10% have negative consequences for the population growth?

To determine the effect of additional mortality from wind turbines populations of species that are vulnerable to wind turbines, we used population models. Using key parameters on mortality and litter size from literature, we formulated species-specific population models.

This allowed us to calculate the effects of mortality rates. We did this by first modelling a population with no additional mortality and afterwards models with 1%, 5% and 10% additional mortality. We then compared the predicted growth rate under these variants. A population with a growth rate of 1 is stable. With a growth rate smaller than 1 it declines and when it is larger than 1, the population increases. We included uncertainty of parameters (confidence intervals) in the model when these were available from the literature.

We were able to model the population dynamics of 6 of the 7 study species. The 6 resulting population models show that for all but one species, the model without additional mortality predicts moderately to slow growth. However, the population model of N. noctula predicts a decline.

For all species the models show a decline at 10% additional mortality. Different additional growth rates had different effects depending on the species (and its vital rates). As expected, some species are stronger affected by additional mortality than others. *Vespertilio murinus* and *Pipistrellus pipistrellus* enter decline between 5 and 10% additional mortality, *P. nathusii*, *Eptesicus serotinus* and *Nyctalus leisleri* between 1 and 5%, and *N. noctula* is predicted to be already declining. *P. nathusii* and *N. leisleri* are most sensitive to additional mortality, as can be seen by the steeper decline in the growth rate. The tipping point, the additional mortality value where the population changes from growing to declining, differs per species.

Although the predictions of the models are uncertain about the exact growth rates, it is clear that additional mortality systematically results in a lower growth rate and may even result in a shrinking population.

So, whether additional mortality will cause a population to shift from growing or stable to declining can only be known when better knowledge on vital rates is generated. The sensitivity analyses of each of the population models show that the parameter with the most impact on the predicted growth rate is adult survival. Improving knowledge and information on the aspect of adult survival in (Dutch) populations of the species vulnerable to wind turbines therefor should be given priority.

Concluding, the models of all species show a declining population when there is 10% additional mortality, but the additional mortality value where the population changes from growing to declining differs per species. Relying on a single rule of thumb to determine acceptable additional mortality is an overly simplistic approach. To sustain populations of bats, additional mortality thresholds need to be calculated for local populations using local data.

1. INTRODUCTION

Individual bats and bat populations are protected under Dutch National laws. A threat to bats that has emerged in the past decades are the energy transition, using wind turbine parks for energy production. The construction and operation of windfarms can negatively impact roosts, foraging sites as well as commuting routes, and can cause mortality when bats collide with the blades of turbines (Arnett et al., 2016). There are indications that turbines attract bats, although the causation of this is still not totally clear (Guest et al., 2022).

For any taxonomic group, it is crucial to understand which portion of the population is affected and, more importantly, the impact of this additional mortality on population trends (e.g., Schippers et al., 2020 for birds), with even greater urgency for bats.

Bat populations are particularly susceptible to increased mortality rates, given the low fecundity of bat species and thus recruitment of juveniles in populations (Racey & Entwistle, 2001). Therefore, even minor increases in mortality risks may have large-scale effects on bat populations.

But the question remains**: does an additional mortality rate of, for example, 1%, 5% or 10% have negative consequences for the population growth**?

Currently, the so-called 1% criterion (Commission of the European Communities, 1993) is applied. In this approach, an additional mortality of 1% of the total annual mortality of the population is seen as having a negligeable effect on the population dynamics. However, this criterion lacks ecological substantiation. It could be far too high, but also far too low. Certainly, the effect will vary between species, depending on population dynamics. Population dynamic parameters include reproduction (fertility, fecundity, reproductive capacity), mortality; migration (immigration, emigration and dispersal). This gap in knowledge of the effect of mortality by wind turbines on the level of bat populations is universally acknowledged (e.g. Schillemans et al., 2021, UNEP/EUROBATS IWG on wind turbines and bat populations, 2021).

It is especially important to fill this knowledge gap, because the Conservation Status of the bat species sensitive to wind turbines in the Netherlands was classified as very or moderately unfavourable or unknown in the latest report to the EU (Table 1, Annex 1). This concerns the following seven species (Limpens et al., 2021, Schillemans et al., 2021): common pipistrelle *Pipistellus pipistrellus*, Nathusius' pipistrelle *Pipistrellus nathusii*, soprano pipistrelle *Pipistrellus pygmaeus*, noctule bat *Nyctalus noctula*, Leisler's bat *Nyctalus leisleri*, parti-colored bat *Vespertilio murinus* and the serotine bat *Eptesicus serotinus*.

Table 1.1: Favourable conservation status of 7 bat species with a higher risk of collisions with wind turbines, occurring in the Netherlands. Source: Habitat Directive article 17 report to the EU 2019. https://cdr.eionet.europa.eu/nl/eu/art17/envxuhrwa/

Species	FCS 2013-2018
Pipistrellus pipistrellus	Unknown
Pipistrellus nathusii	Unfavourable - Inadequate
Pipistrellus pygmaeus	Not assessed
Nyctalus noctula	Unfavourable - Bad
Nyctalus leisleri	Unknown
Vespertilio murinus	Unfavourable - Inadequate
Eptesicus serotinus	Unfavourable - Inadequate

Aims of the study

The aims of this study are:

- gathering more knowledge about the population dynamics of the target species.
- providing a clearer picture of the - available data of the - population dynamic parameters.
- assess the quantitative effect of wind turbine collision victims on the population dynamics and ultimately the population size of the target species of the NIEWHOL programme.

This is done by developing population models, which are parameterised with values from the literature. Such an approach has been employed in assignments from provinces and the national government, including determining management strategies for fallow deer (Dekker, 2021), stone marten (Dekker & Jonge Poerink, 2022), wolves (Dekker, van den Brink & Boerma, 2024) and various bird species (Schippers et al., 2020). In Germany, this approach has also been applied to bats (Korner-Nievergelt et al., 2018). Subsequently, the impact, of a certain mortality rate caused by wind turbines, or mitigation or additional measures that would strengthen the population (mitigation / compensation) on the population, can be tested in the model.

Disclaimer: model limitations

The outcomes of this model-based approach (population dynamics model) are indicative. Population models are highly dependent on the availability of accurate local data to make reliable predictions. The higher quality parameters are included, in terms of accuracy and applicability to the population being modelled, the closer the predictions will align with reality. However, a population model is still a simplified representation of reality and cannot fully capture the unpredictability of population dynamic in the real world. The models presented here are parameterised with parameters from local studies in sometimes very different areas in Europe, meaning outcomes can differ from population dynamics in the Netherlands. Due to limited high-quality data for all parameters.

This report explains how the application of this and other available models should be interpreted. It is important that no definitive conclusions are drawn from the results presented here, and that readers understand this is an exploration of potential population dynamics.

Relationship with other NIEWHOL work packages

Within the research program of NIEWHOL (2021-2024), a new protocol for monitoring casualty risk in wind farms is also being developed (Klop et al.,2024), and there are proposals for research into spatial risk analysis and migration prediction. The aim of the program is to fill knowledge gaps to achieve better curtailment provisions, where shutdown is only applied when necessary for the population.

Monitoring casualty risk in combination with knowledge about additional mortality is a crucial input in assessing a (potential) effect of wind farms on bat populations. Monitoring of casualty risk involves a research effort where financial and practical feasibility are weighed against the desired accuracy of the estimates. Understanding the population dynamic parameters of the target species is an important factor in estimating the (minimum) required accuracy of the casualty risk estimates through monitoring.

The spatial risk analysis is initially an analysis of the 'relative casualty risks in different landscapes and regions.' Understanding differences in risks between different landscapes and regions is important in making location choices in the wind farm development process. When this is combined with knowledge of factors such as population size and population dynamic parameters, differences in risks between landscapes and regions can be interpreted as differences in effects on the population.

2. MATERIAL AND METHODS

GENERAL APPROACH

To determine the role of additional mortality from wind turbines in the population dynamics of species that are vulnerable to wind turbines, knowledge of population dynamics is essential. This involves numerical data for parameters such as reproductive age, reproduction, mortality, migration, and dispersal. We do this through a review of the literature, including relevant ‘grey’ literature.

When these key parameters are available, we formulate species-specific population models. This allows us to also calculate the effects of mortality rates. We do this by first modelling a population with no additional mortality, and then adding 1%, 5% and 10% additional mortality. We then compare the predicted growth rate under these scenario's, called λ. With a λ of 1, a population is stable. When it is smaller than 1, the population declines. When it is larger than 1, the population increases. We include uncertainty of parameters (the confidence intervals) in the model when these are reported.

This process leads to reliable models that make concrete predictions about the effect of added mortality on populations. These predictions are the goal of the study.

In the following paragraphs, we give more details on the modelling strategy, the assumptions and limitations of the models used, and their implementation.

MODEL STRUCTURE

For this study, Leslie matrix models are used. This is a classic discrete age-stage-structured model of population growth. Leslie models distinguish classes of ages, stages and/or sexes (Leslie, 1954), where each age-stage class is explicitly modelled. For bats, a sensible stage structure consists of juveniles, 1year olds, and of 2 years and older, and to separate females and males in these groups.

Matrix models are an often-used type of model for species where different life stages are relevant for understanding population dynamics (Caswell, 2001; Schippers et al., 2020; Schaub & Kéry, 2022). Using matrix models. populations of thousands of species have been modelled (see database https://compadre-db.org/).

The model is structured to take time steps of 1 year. The modeller can choose for a census moment directly before or after the birth of offspring. This allows alignment with monitoring surveys. Other attractive features of these models are:

- The models provide insight into which characteristic (litter size, survival of stage 1, 2, or 3, etc.) is most important in population dynamics.
- Additional mortality can be added relatively easily.
- It is relatively straightforward to determine the effect of natural variation in survival or reproduction on population dynamics.
- With these models, it is possible to determine which parameters (and thus which species-specific population characteristics) are sensitive to the effect of inaccuracies

of the model parameters on the ultimate accuracy of the outcomes. This is done with so-called sensitivity and elasticity analyses. Subsequently, a range of the precision of the predicted population effects can be provided with these models.

Age structured models - simple to more complex

To model the populations of the 7 species of bats, we adapt the model structure to the available data for each species. The simplest form of this is a model with two stages: juveniles and adults (figure 2.1).

Within the two-stage model the recruitment is the number of female adults that survive the year to reproduce s_{ad}, times the average number of juveniles per female b. For example, if there are 100 female adults in year 1, the annual survival is 80%, and the females in the population produce on average 2 offspring, the recruitment is 100x0.8x2 = 160 juveniles. The number of adults is the fraction that survives the year s_{ad} plus the juveniles that survive the year s_{juv} and become adults. So, when there are 200 adults and 100 offspring in year 1, the survival of adults is 80%, and the survival of juveniles is 50%, the number of adults in the next year will be 200 x 0.8 + 100 x .5 = 210 adults. This resulting number is then used to calculate the number of adults and females in the next year. Such a calculation can be done for example for 30 years to simulate the population dynamics.

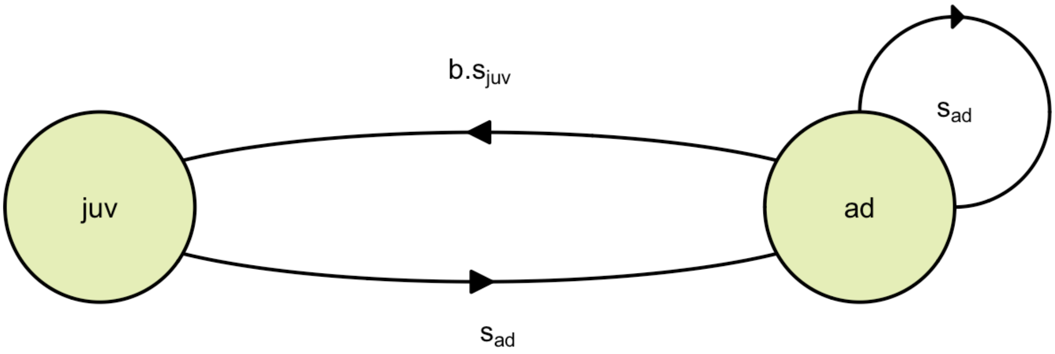

Figure 2.1. A simple two-stage population model for juveniles and adults.

The model can be expanded to model for example juvenile, yearling and adult life stages, and for females and males separately (figure 2.2). We only do this where stage-specific survival rates were available.

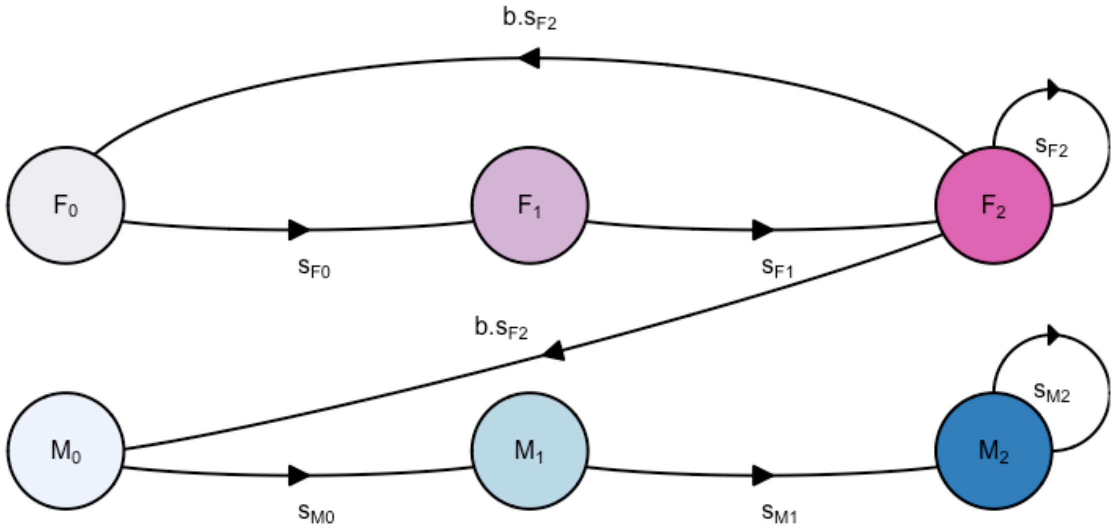

Figure 2.2. A more complex stage-age structured model with different age classes and females and males modelled separately. In this variant, only females that are 2 years or older reproduce. b is the number of female or male offspring per female (assuming an equal sex ratio). s are annual survival rates.

There is an additional benefit of Leslie models: it is easy to calculate the sensitivity of the model to small changes or errors.

The availability of information limited the complexity of the models. For some species only the most basic information (adult survival, litter size) could be found, whilst for others, we found litter size mean and spread, and annual survival rates for females and males in different age class. We preferred to let the information available determine the complexity of the model, instead of using one complex model and guessing parameters for the less intensively studied species.

We discuss the models per species in chapter 3, in order of complexity of the model.

Stochasticity from natural variation and parameter uncertainty

Often, only an average litter size or survival rate was given by the sources. For birth rates for example, in several cases not even an average birth rate could be found (i.e. "the species usually has one young, but sometimes twins"). However, some sources did report average values and confidence intervals or even gave frequency tables.

When confidence intervals or variances are given, models are formulated to include this stochasticity in the parameters. This is done by running the models 10.000 times (replications) for 30 steps (years) each. In each run, random values from a Beta-distribution (for survival values) are selected. This way the effect of uncertainty on the results are made visible. If confidence intervals for litter size are provided, also the uncertainty or natural variation in litter size can be included in the model, by taking random values from a Poisson distribution at each year or even each individual.

The models are parameterised with field data on vital rates: number of offspring per female and annual survival rate. For many organisms, approximations or actual data of reproduction and survival are available because they are (relatively) easy to derive from counts and ringing or other mark-recapture studies.

Assumptions and limitations of the stage-structured models

When making predictions of population developments, certain principles, mechanisms and assumptions about the population dynamics of the species(s) are always used. In the case of these population models, the most relevant assumptions and simplifications are:

- The model is not spatially explicit: the habitat itself is not modelled. This means that spatial aspects (e.g. spatial distribution of roosts, food, and mates) that may influence survival or birth in a real population are neglected.
- We model a population scaled to 1. When actual population sizes are known, the models can be run using the actual population sizes..
- We have not modelled positive or negative density-dependent factors or processes. A well-known density dependence process is the emergence of competition for food, which causes poorer body condition, in turn resulting in less reproduction and/or higher mortality, or emigration by some of the animals. Such negative density depended processes cause a decrease in growth rate and ultimately cause a (fluctuation around the) carrying capacity of an area. An example of positive density dependence are energetic benefits, such as the clustering of young animals together while the mothers hunt. Both positive and negative density dependence are not included in the model due to the lack of solid quantitative data for bat populations.
- In many mammals, it has been found that reproduction decreases with age. This has not been modelled, because no quantitative data on this process was found in the literature for the target species.
- Interaction with other species is not included. It is assumed, that competition for food or roosts is not a limiting factor for bats in the Netherlands, and death by predation is already included in the annual survival rates found in the literature.

Implementation

All models were implemented in statistical environment R 4.14 (R core team, 2024) using scripts for reproducibility.

PARAMETERISATION

We started with an overview of what the most important determining parameters were for the model. We listed which values are known for the study species as well as of which relevant parameters, no or insufficiently exact values are known.

To draw up population models of NIEWHOL's target species we first reviewed available data from literature, databases, and available field data and counts. There is a lot of data for litter size in the (grey) literature and several suitable sources have report annual survival. In addition, we used the COST Action ClimBats (https://climbats.eu/) database. Various life history parameters have been collected here, including litter size and maximum established ages (https://jasja.shinyapps.io/ClimBats/). In addition, we screened the Handbook of

European Mammals (Russo, 2022) - this contains a lot of grey literature, possibly also about survival, number of young and other relevant population dynamics parameters.

In our literature review, we looked for the following parameters:

- annual survival or mortality rates

- percentage of females reproducing

- litter size: number of offspring per female

- the number of females that reproduce and the number of offspring together are the *fecundity*.

We recorded the parameter, confidence intervals (when given), method used (when given), region the study was performed and of course reference to the paper.

For some sources, additional analyses were needed. Some studies gave confidence limits for the parameters. As we needed standard deviations to include these uncertainties in the models, these ranges were recalculated. For this we assumed a Beta-distribution for survival rates and calculated the standard deviations. This is slightly more precise than assuming a normal distribution.

For some species estimates for the parameters were available from different studies. In these cases, we selected the parameters we found most fitting for this study of Dutch bats populations. We give our motivation in the results section.

ANALYSIS AND PERTURBATIONS

Growth rate and projections

Once the model was formulated and parameterised, we calculated the population growth and growth rate. This can be derived from a property of the population matrix. One of these properties uses the characteristic of matrices called the eigenvalue. An eigenvalue is a number associated with a square matrix that tells you how much a certain direction is stretched or shrunk when the matrix is applied to a vector. The so-called dominant eigenvalue of a population matrix summarizes the annual growth, called λ, of the modelled population. A λ of 1 is a stable population: it does not increase nor decrease. A λ higher than 1 stands for a model with a growing population. A λ lower than 1 indicates that the modelled population decreases. The annual growth is the base for the analysis of the models and the changes in this value show the effects of additional mortality on population dynamics. An example is given below: here, matrices with different λ are given. It shows that a λ below 1 represents a decreasing population. A λ above 1 represents a growing population.

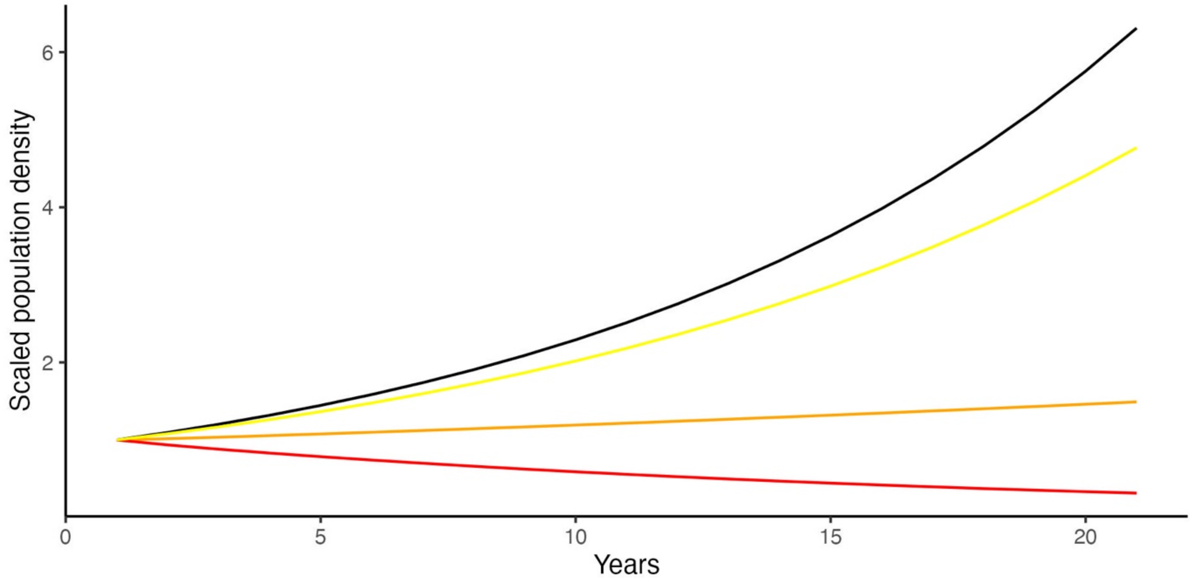

Figure 2.3 Projection of a population using matrix models with four different λ, in this case Vespertilio murinus. Black: $\lambda = 1.096$. Yellow: $\lambda = 1.081$ Orange: $\lambda = 1.021$ Red: $\lambda = 0.950$. See chapter 3 for the model.

Sensitivity and elasticity analysis

We performed sensitivity and elasticity analyses to 1) understand which life history traits have the most effect on population growth, and 2) to understand what effect the uncertainty (confidence intervals) of the parameters has on our predictions.

Sensitivity measures the effect of small changes in the model parameters (the matrix elements) on the population growth λ. A higher sensitivity value suggests that a small change in that specific demographic rate will have a larger impact on the population growth rate. A lower sensitivity value implies that changes in the corresponding demographic rate will have a smaller effect on λ. It is the change in growth rate $\delta\lambda$ divided by the change in a parameter $\delta a_{i,j}$

$$S_{ij} = \frac{\partial \lambda}{\partial a_{ij}}$$

Sensitivity can be calculated analytically or using Monte Carlo simulations.

Sensitivities give the absolute effect of changes in a parameter which is scaled to indicating how a 1% change in a parameter affects λ by percentage. This is called the elasticity of the model and allows comparison between different types of parameters (change in survival versus change in litter size) and comparisons between models. Elasticities give insight into the proportional importance of each parameter. For example, a higher elasticity for juvenile survival than for adult survival would suggest that the population growth rate is more responsive to changes in juvenile survival. To formulate recommendations for future work, we use the elasticity.

In this study, the sensitivity and elasticity analysis were analysed following Caswell (2001: page 208, as implemented by R library "Popdemo").

Perturbations

Using the models, we tested the effects of "perturbations": additional mortality (due to wind turbines). This was done in one of two ways. For models without stochasticity, we modify the survival rates in the model: subtracting 1 (0.01), 5% (0.05) or 10% (0.10) from the annual mortality rates and evaluating the effect on growth rate λ analytically. So, if the measured survival was 80%, i.e. 0.8, the mortality is 0.2. Additional mortality of 1% decreases annual survival from 80% to 79%, or from 0.8 to 0.79. Note that this is different from the ORNIS-criterion approach. There a 1% of the mortality is used, so if mortality is 20% or 0.20 of the population, applying the Ornis criterion results in a mortality of 0.202 (1% of 0.20 is 0.002). For models with stochasticity again λ was calculated using Monte-Carlo simulations. So, we use percentage points and not percentages. This was done for practical reasons.

For species where the model does not include stochasticity λ was simply calculated from the adapted matrix model. For these species, we also calculated the effect of a continuous range of 0 to 10% additional mortality and plot the resulting λ as a function of the additional mortality. We did this in two variants: all stage-age classes have an equal additional mortality, or juveniles have double the additional mortality of adults. So, if the additional mortality rate of adults is 5% (or 0.05 subtracted from the annual survival rate), the additional mortality of juveniles is 10%.

RECOMMENDATIONS FOR FILLING KNOWLEDGE GAPS

During literature review and model formulation and analysis, we identified which knowledge gaps have been found in respect to population parameters, and what their relative importance is for gaining insight into effects on the populations of the relevant species. We report if and how these gaps can be filled (for example by analysing existing data that have not yet been obtained and processed; or through targeted fieldwork). These recommendations are based on their relative importance in the model predictions but are also based on the expected effort for collecting and analysing data, advice is given as to which knowledge gaps should be addressed with priority.

3. RESULTS

PARAMETER COMPLETENESS AND MODELS USED

From literature, we were able to find litter sizes and (apparent) annual survival rates for all species but *Pipistrellus pygmaeus* (table3.1, table 3.2). A smaller number of studies also reported uncertainty (confidence intervals) for the survival rates.

Table 3.1. Data completeness. Given are the number of parameters values we found for (apparent) survival rates, fraction reproducing females and litter size per species

Species	Annual survival	Fraction reproducing females	Litter size
Eptesicus serotinus	7	1	3
Nyctalus leisleri	11		3
Nyctalus noctula	4	1	5
Pipistrellus nathusii	3		5
Pipistrellus pipistrellus	12		4
Pipistrellus pygmaeus	2		1
Vespertilio murinus	3	1	4

As we formulated the models according to availability of parameters, the literature review led to different models for different species, from very simple to quite complex (table 3.2). Stochasticity was included in 4 of 6 models. The results are discussed per species in the paragraphs below, in order of increasing complexity of the respective models.

Table 3.2. A simple two-stage population model for juveniles and adults.

Species	Model structure	Stochasticity included?
Pipistrellus pygmaeus	no model possible	-
Vespertilio murinus	2 stages - 2 sexes	No
Pipistrellus nathusii	2 stages - 2 sexes	No
Pipistrellus pipistrellus	2 stages	Uncertainty of survival
Eptesicus serotinus	2 stages, females only	Uncertainty of survival
Nyctalus noctula	2 stages, females only	Uncertainty of survival
Nyctalus leisleri	3 stages - 2 sexes	Uncertainty of survival

In the following paragraphs, we discuss the parameters and model structure for each of the species. We then analyse the model and the effect of perturbations (i.e. additional mortality) on the population growth rate. In the final paragraph of this chapter, we present an overview of the results of the perturbation analyses.

Foto: Erik Korsten

PIPISTRELLUS PYGMAEUS

Parameters and model structure

For parameterising the model for *Pipistrellus pygmaeus*, we used the data gathered by Gerell & Lundberg (1990). The authors published the paper as a study on *Pipistrellus pipistrellus*, before *P. pygmaeus* was first identified. Jones & Froideveax (2023) concluded from the ranges of the species of the Pipistrellus complex in Europe, that this study must have been *P. pygmaeus*. They report a litter size of one.

Gerell & Lundberg (1990) report annual survival rates and their variance for adult females and males and an overall average survival rate for adults (table 3.3). Unfortunately, they do not report confidence intervals of the latter. They also do not report the survival rate for juveniles, and we did not find survival rates for juvenile *P. pygmaeus*. Without values for the annual survival of juveniles, we cannot formulate a meaningful model.

Table 3.3 Population dynamics parameters for Pipistrellus pygmaeus.

Parameter	Age/stage	Value	Source
litter size		1	Jones & Froideveax (2023)
survival rate	juvenile	-	No data found
survival rate	female adult	0.54	Gerell & Lundberg 1990)
survival rate	male adult	0.44	Gerell & Lundberg 1990)

Foto: Erik Korsten

VESPERTILIO MURINUS

Parameters and model structure

To parameterise the population model for *Vespertilio murinus*, we used the data gathered by Safi (2006) in a breeding colony in Switzerland. Safi (2006) estimated annual survival rates as a fraction of the number of animals marked in year t to the number caught again in year t+1. Within the scope of our project, it was not feasible to make the data of individual animals available to estimate annual survival rates using mark-recapture models for open populations. We could not find annual survival rate of male juveniles. For the model, we assume a survival rate equal to that of female juveniles for this group.

Litter size is given as 1.8 young per female (Zhigalin & Moskvitina 2007).

Using marked animals and return rates, Safi (2006) reports a fraction of reproducing females in the colony of 87%. No confidence intervals were reported for any of the parameters.

The available parameters (table 3.4) permitted us to formulate a model with juvenile males and females and adult males and females (figure 3.1), without stochasticity.

Table 3.4. Population dynamics parameters for Vespertilio murinus.

Parameter	Age/stage	Value	Source
fraction reproducing	adult female	0.87	Safi (2006)
litter size	-	1.8	Zhigalin & Moskvitina (2007)
survival rate	female adult	0.76	Safi (2006)
survival rate	male adult	0.42	Safi (2006)
survival rate	female juvenile	0.62	Safi (2006)
survival rate	male juvenile	0.62	assumption

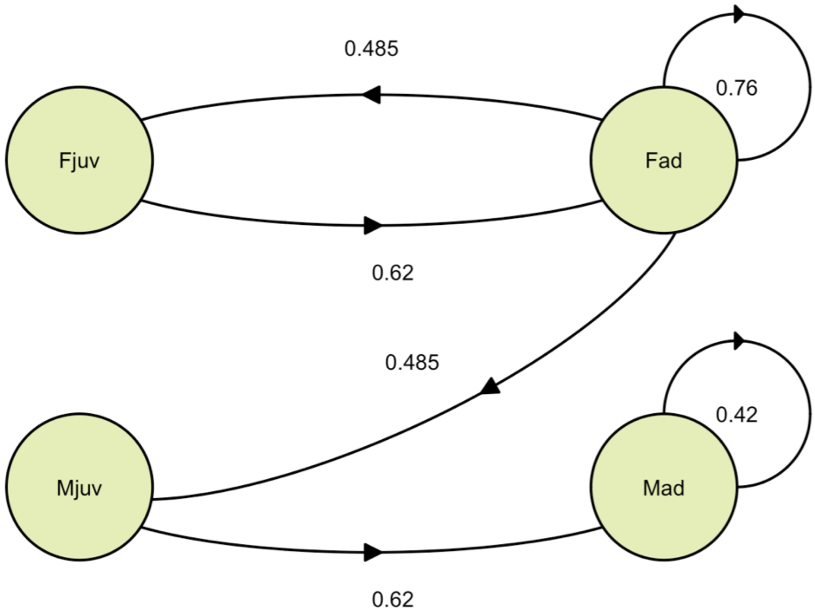

Figure 3.1 The parameterised population model for Vespertilio murinus.

Model analysis and projection

The simple model without stochasticity was analysed analytically. The population shows positive growth per year: 4.7% increase per year ($\lambda = 1.047$). The population growth is most sensitive to changes in the survival of adult females (see paragraph "Overview of sensitivity analysis"), with an elasticity of 0.53.

Perturbations - effect of additional mortality

For this analytical analysis, the additional mortality is taken from each of the survival rates. So, if the natural survival rate is 0.62 for juvenile females (62% percent of the females survive their first year), an additional 10% mortality means the annual survival rate becomes 0.52 (52% of the juvenile females survive their first year).

First, we give an example of the development of a population over 20 years to illustrate how growth rate λ summarizes the growth or decline of a population. With no additional mortality, the population growth rate is 1.047. At 1% additional mortality, divided over the stages, the population growth declines to λ=1.032. At 5% additional mortality, the population growth λ is 0.972 and at 10% additional mortality the population growth λ declined to 0.897per year. So, in fact, a shrinking population (figure 3.2).

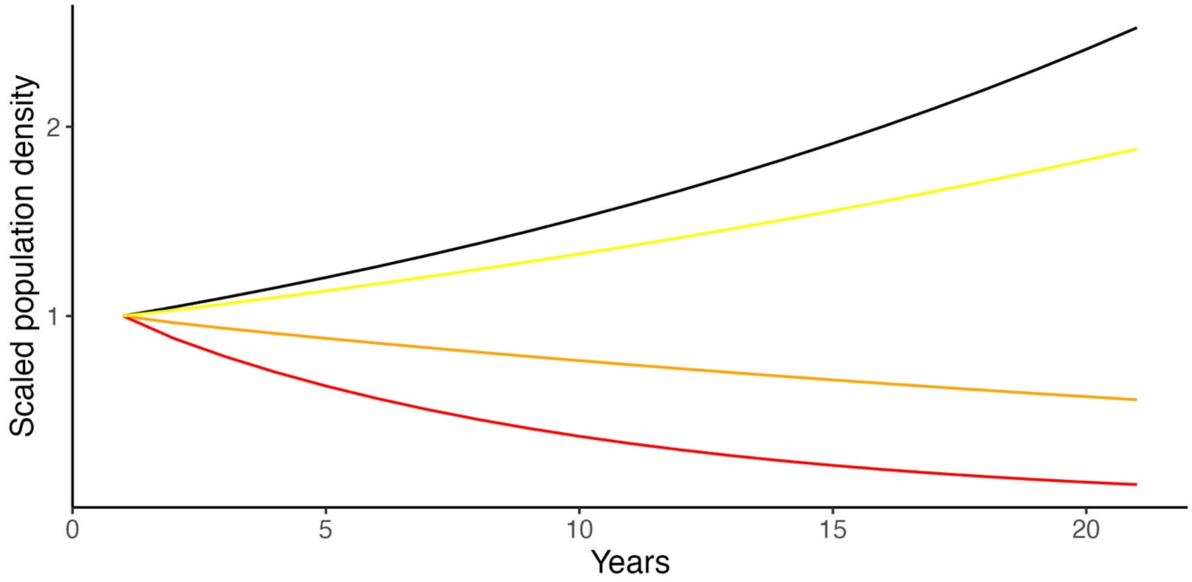

Figure 3.2 Projection of a population of Vespertilio murinus *over 20 years, scaled to 1.*
Black: no additional mortality, $\lambda = 1.047$
Yellow: 1% additional mortality at each stage-sex class, $\lambda = 1.032$
Orange: 5% additional mortality, $\lambda = 0.972$
Red: 10% additional mortality., $\lambda = 0.897$

Next, we calculated the effect of additional mortality in three scenarios:

- additional mortality under juveniles only,
- additional mortality under adults only,

- additional mortality under juveniles and adults.

In graph 3.3., we show the growth rate of the population under these scenarios. When growth rate λ falls below 1, the population does not grow. Additional mortality affects the growth rate in all three scenarios. For the scenario when all ages and sexes are affected by the additional mortality, the population declines from about 6.3% additional mortality. When only adults are affected, this is the case at around 8.7% additional mortality.

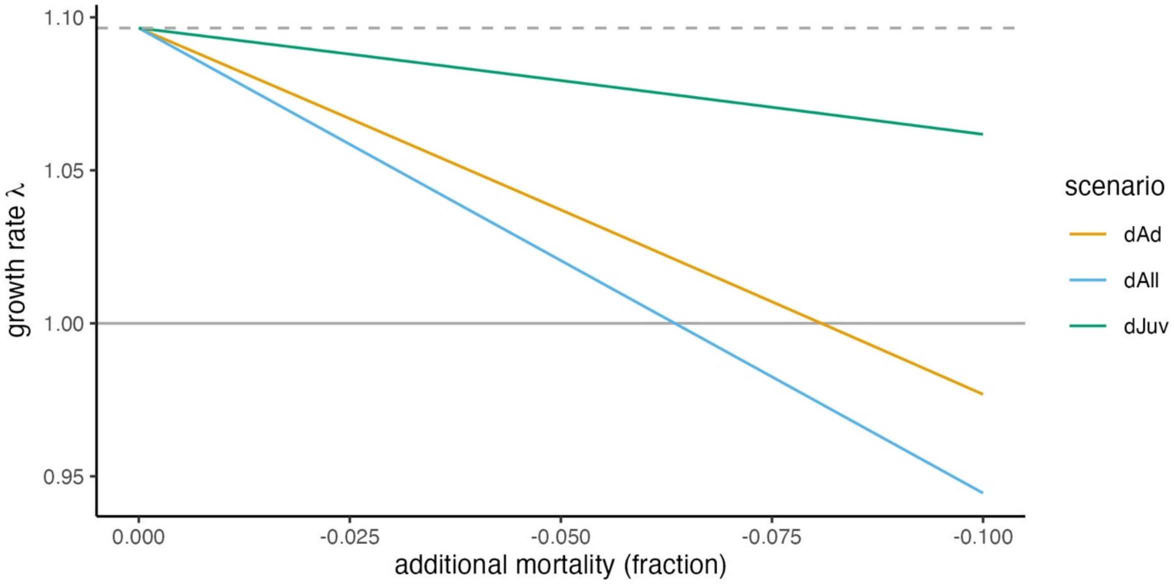

Figure 3.3. Population growth rates for Vespertilio murinus under a scenario of different additional mortalities: for adults only, for juveniles only, or for all stages. Dashed line: growth rate when there is no additional mortality. Horizontal black line: stable population.

Foto: *Erik Korsten*

PIPISTRELLUS NATHUSII

Parameters and model structure

The litter size of Nathusius pipistrelle *Pipistrellus nathusii* is reported as 1.9 (Schmidt 1994a, 1994b) offspring per female. Three other authors report a litter size of two (Hacketal, 1984; Natuschke, 1960; Alekperov, 1980; in Vierhaus, 2001).

Schmidt (1994a, 1994b) gives annual survival estimates for juvenile females (68% per year), female adults (70,8%) and male adults (at least 60.7%), with no confidence intervals.

We did not find information about the fraction of adult females that reproduce annually.

When we assume that:

1) the (unreported) apparent survival rate of juvenile males is equal to that of juvenile females, and

2) the litter size is based on **all** adult females in the population and not only reproducing females,

we can use the available parameters (table 3.5) to build a model with 4 stages: juvenile females, juvenile males, adult females and adult males (figure 3.4). The model does not include stochasticity.

Table 3.5. Population dynamics parameters for Pipistrellus nathusii. -: no sources found.

Parameter	Age/stage	Value	Source
fraction reproducing	female adult	-	
litter size		1.9	Schmidt (1994a, 1994b)
survival rate	female adult	0.708	Schmidt (1994 a, 1994b)
survival rate	male adult	0.607	Schmidt (1994 a, 1994b)
survival rate	female juvenile	0.680	Schmidt (1994 a, 1994b)
survival rate	male juvenile	-	
survival rate	male juvenile	0.680	assumed

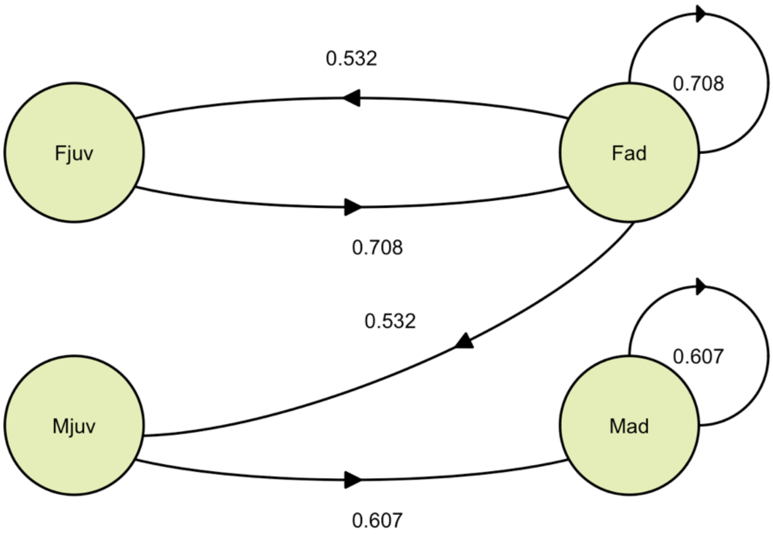

Figure 3.4 Structure of the population model for P. nathusii.

Model analysis and projection

The simple model without stochasticity could be analysed analytically. Growth rate λ is the first eigenvalue of the Leslie matrix. The population shows a positive growth of 6.2% per annuum (λ = 1.062).

The population growth is most sensitive to changes in the survival of adult females (elasticity of 0.500).

Perturbations - effect of additional mortality

As with the model for *Vespertilio murinus*, the additional mortality is taken from each of the survival rates. First, we give an example of the development of a population over 20 years. With no additional mortality, the population growth rate is 1.062. With 1% additional mortality, divided over the stages, the population growth rate declines to 1.046 per year. With 5% additional mortality it is 0.983, and with 10% additional mortality, divided over the stages, the population growth rate declines to 0.902 per year. This results in declining populations with 5% and 10% additional mortality (figure 3.5).

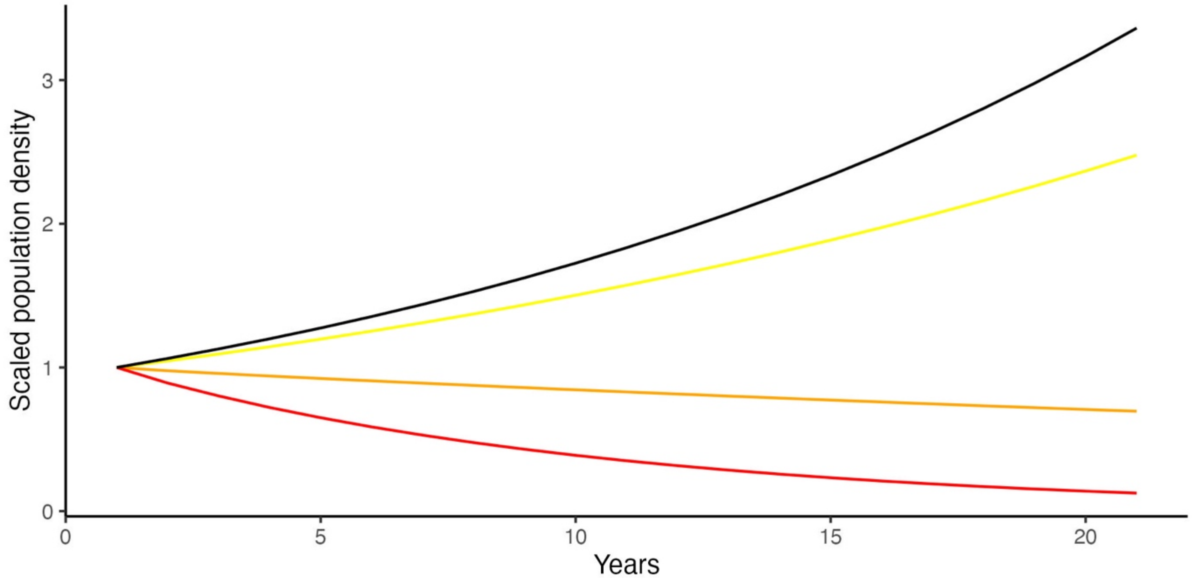

Figure 3.5 Projection of a population of Pipistrellus nathusii over 20 years, scaled to 1. Black: no additional mortality, yellow: 1% additional mortality divided proportionally over stages/sexes, orange: 5% additional mortality; red: 10% additional mortality.

Next, we calculated the effect of additional mortality in three scenarios.

- additional mortality under juveniles only (as juveniles are more sensitive, as described by Kruszynski et al. (2022).

- additional mortality under adults only,

- additional mortality under juveniles and adults.

In graph 3.6., we show the growth rate of the population under these scenarios. When growth rate λ falls below 1, the population does not grow. Additional mortality affects the growth rate in all three scenarios. For the scenario when all ages and sexes are affected by the additional mortality, the population declines at around 4% additional mortality. When only adults are affected, this is the case at around 5.5% additional mortality.

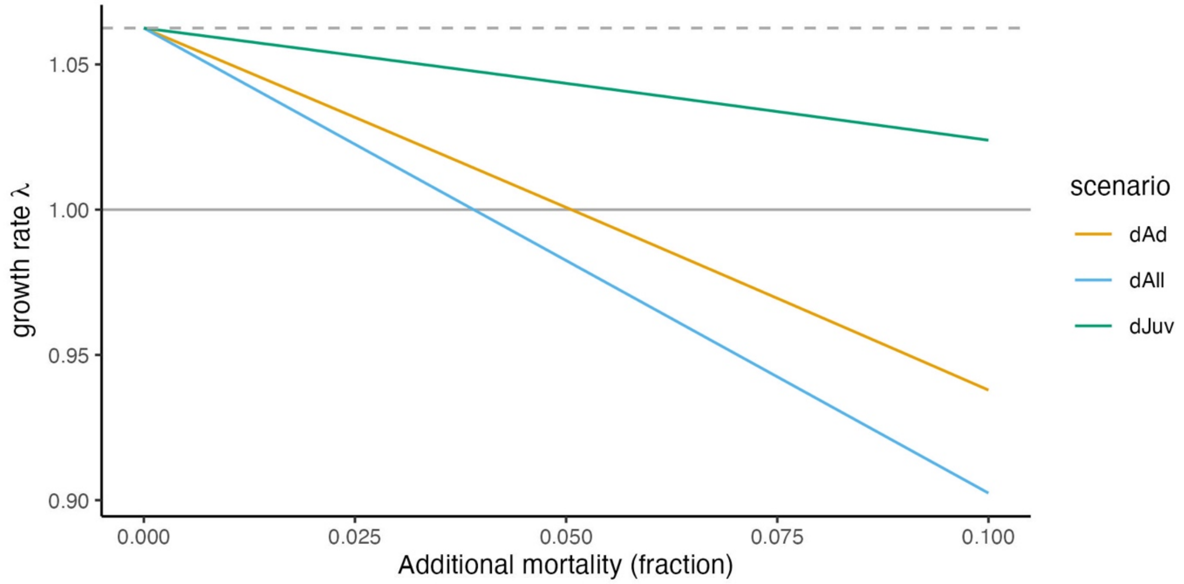

Figure 3.6. Population growth rates for Pipistrellus nathusii under a scenario of different additional mortalities: for adults only (dAd), for juveniles only(dJuv), or for all stages (dAll). Dashed line: growth rate when there is no additional mortality. Horizontal grey line: stable population.

Foto: Wesley Overman

PIPISTRELLUS PIPISTRELLUS

Parameterisation

Pipistrellus pipistrellus is probably the most common bat species in western Europe, and there are quite a few survival rates and litter sizes reported. Sendor & Simon (2003) report survival rates with confidence intervals for juveniles and adults. The data are based on a ringing study in Germany. They also show survival rates for juveniles and adults per sex in figures, but without confidence intervals and do not give these exact values in the text. Lopez-Roig & Serra-Cobo (2014) give survival rates for juveniles and adults per sex but find very low survival rates and large confidence intervals for the juveniles. This is possibly because survival and emigration cannot be separated when the study area is small, or dispersal distances are large.
Thompson (1987) reports a survival rate of females of 0,64 from the Vale of York based on a ringing study in the late 1970s and early 1980s.

To parameterise the population model for the species, we used the survival parameters for adults and juveniles from Sendor & Simon (2003).

Litter size is reported to be 1, 1.16, 1.2, or 1.7 young per female (Dietz et al., 2009; Eichstädt upublished, in Eichenstäd & Bassus, 1995; De Magaelhaes & Costa, 2009; Haarsma & Siepel, 2006). None of the authors reported a confidence interval. We chose the litter size of 1.7 from the Dutch source for our further modelling, as this is the only source from the Netherlands. There is not a lot of information about the fraction of females in the population that reproduce. The two sources reported a wide range, from 7.1% to 28.2% (Racey, 1969 respectively Hurka, 1966 in Taake & Vierhaus, 2001) and were based on 1 season and a small number of animals.

It is then assumed that the average litter sizes are calculated per adult female, considering the fraction of females that do not breed.

The available parameters (table 3.6) allowed us to formulate a model with juvenile and adult females only (figure 3.7). This means that, assuming an equal sex ration, the litter size for the model becomes 1.7 / 2 to calculate the female offspring per adult female. We can include stochasticity to take into account the reported uncertainty in the survival rate estimates.

Table 3.6. Population dynamics parameters for Pipistrellus pipistrellus.

Parameter	Age/stage	Value (sd)	Source
fraction reproducing	female adult	7.1 - 28.2% - not used	Racey, 1969; Hurka, 1966
litter size		1.7	Haarsma & Siepel, 2006
survival rate	adult	0.799 (0.051)	Sendor & Simon, 2003
survival rate	juvenile	0.527 (0.095)	Sendor & Simon, 2003

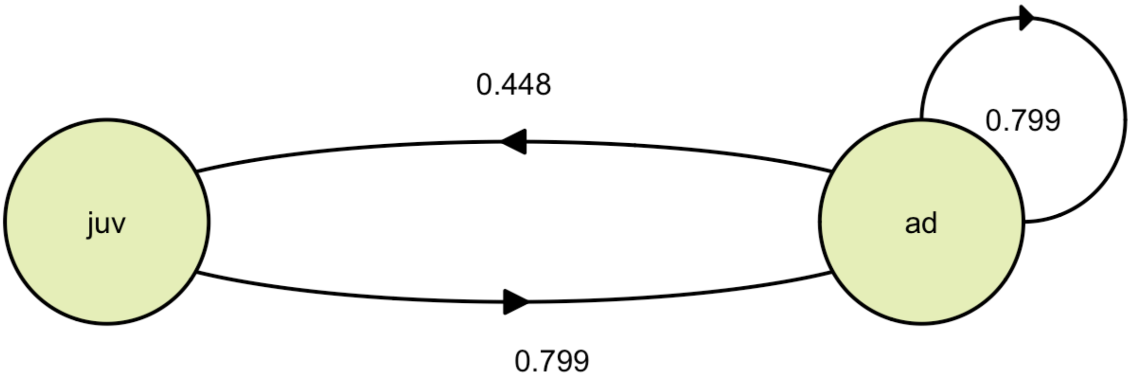

Figure 3.7 Structure of the population model for P. pipistrellus

Model analysis and projection

First, we analysed the static Leslie model the classical way. The analytical growth rate λ is 1.119. The sensitivity analysis shows that the model is most sensitive to changes in adult survival, with an elasticity of 0.55 and an elasticity of 0.2223 for both juvenile survival and reproduction.

Next, we included parameter uncertainty by generating survival rates from a Beta distribution with the means and standard deviations in the table above. Using these, we calculated the growth rate, sensitivity of the growth rate to juvenile and adult survival rate changes for those parameter values. We did this 10.000 times, each time with newly generated parameter values. The results of this Monte Carlo simulation were then summarized and plotted as frequency plots (figure 3.8). The model shows a population growth rate λ of 1.117 (±0.0716) when uncertainty in the survival parameters is considered.

Perturbations - effect of additional mortality

In the study of the effect of additional mortality on the growth rate, we considered different scenarios. We looked at additional mortality rates of 1%, 5%, and 10% for all stages. This was done by subtracting the additional mortality from the mean survival. The resulting growth rates are given in figure 3.8) and summarised in table 3.7. Between 5% and 10% additional mortality, the mean growth rate drops below 1 and the population declines.

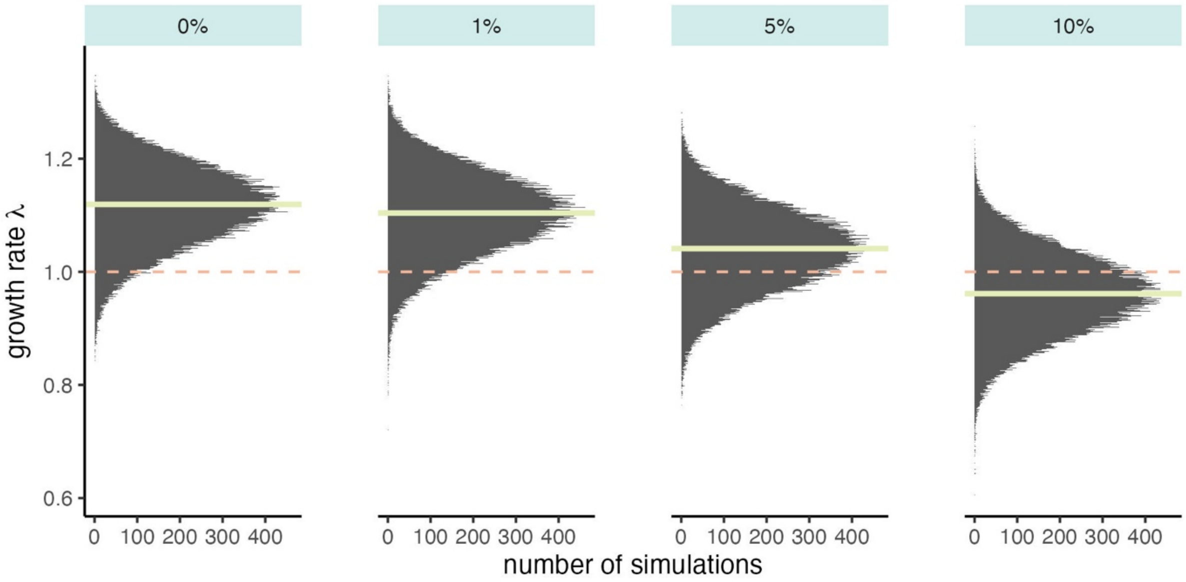

Figure 3.8. Growth rate of Pipistrellus pipistrellus *under different additional mortalities of 0% to 10%. Shown are the resulting growth rates λ from 10.000 simulations for each scenario. Green line: median growth rates. Dashed red line: population growth 1, i.e. stable population.*

Table 3.7. Monte Carlo simulation mean, standard error and 25 and 75% quantiles of the growth rates λ under different additional mortalities of 0% to 10% for Pipistrellus pipistrellus.

Scenario	mean	MC-s.e.	Q25	Q75
0%	1.1172	0.07189	0.9691	1.251
1%	1.1018	0.07163	0.9560	1.236
5%	1.0392	0.07206	0.8938	1.176
10%	0.9606	0.07219	0.8173	1.100

Foto: Wesley Overman

EPTESICUS SEROTINUS

Parameters and model structure

To parameterise the population model for *Eptesicus serotinus*, we used the data gathered by Chauvenet et al. (2014). They used capture-mark-recapture analysis to estimate survival for female juveniles and breeding females in two colonies. For the model, we select the estimates for a colony with the highest survival (0.8 instead of 0.72 for juveniles, 0.77 instead of 0.75 for breeding females.

Litter size is reported to be 1.3 young per female, 1.5 or 1 (Haarsma & Siepel, 2013, De Magaelhaes & Costa, 2009 and Dietz et al., 2009 respectively). For none of these litter sizes an error term was provided. We chose the median value for litter size of 1.3 for the model. It is then assumed that the average litter sizes are per adult female, taking into account the fraction of females that do not breed.

Martolini et al. (2023) report that only 65% of the adult females takes part in the reproduction, and Haensel (1994; in Bagøe, 2001) reports that the females of the species first reproduce in their second year.

The available parameters allowed us to formulate a model with juvenile and adult females (figure 3.9), with stochasticity to include the uncertainty in the survival rates in the model predictions. This means that, assuming an equal sex ration, the litter size for the model becomes 1.3 / 2 to calculate the female offspring per adult female. We were unable to formulate a model that splits females into 1 year and 2+ years old. We assume that the fraction of females reproducing reported by Martolini et al. (2003) represents these 1-year-old (and a number of 2+ year old) non - reproducing females.

Table 3.7. Vital rates for Eptesicus serotinus *adult female-juvenile female population model. s.e.: standard error. It is assumed that that fraction of the female population that is reproducing is included in the number of births per female.*

Parameter	Age/stage	Value (s.e.)	Source
fraction reproducing	females	0.65	Martolini et al., 2023
litter size (b)	Females per female	1.3 /2	Haarsma & Siepel, 2013
survival rate (s_{ad})	female adult	0.77 (0.07)	Chauvenet et al., 2014
survival rate(s_{juv})	female juvenile	0.80 (0.12)	Chauvenet et al., 2014

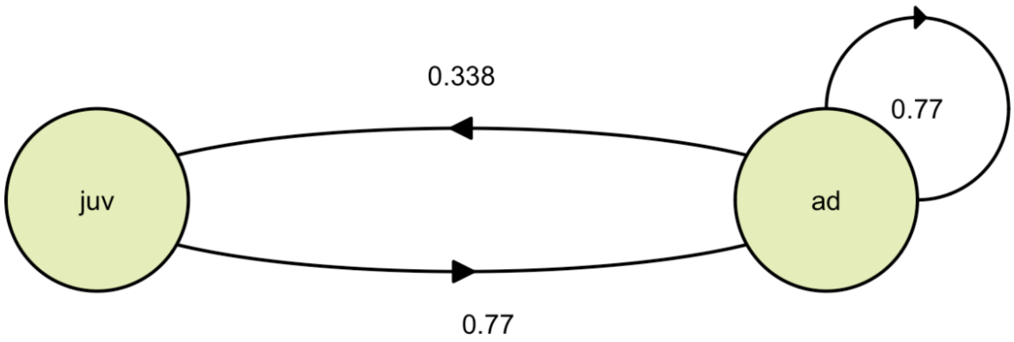

Figure 3.9 The population model structure for Eptesicus serotinus.

Model analysis and projection

The approach is similar to the previous species.

First, we analysed the static Leslie model the classical way. Growth rate λ is 1.024. The sensitivity analysis shows that the model is most sensitive to changes in adult survival, with an elasticity of 0.602 and 0.199 for both juvenile survival and reproductivity.

Next, we included parameter uncertainty by generating survival rates from a Beta distribution with the means and standard deviations in the table above. Using these, we calculated the growth rate, and the impact of additional mortality on the growth rate to juvenile and adult survival rate changes from the population model for those parameter values. We did this 10.000 times, each time with newly generated parameter values. The results of this Monte Carlo simulation were then summarized and plotted as frequency plots (figure 3.10). The model shows a population growth rate λ of 1.023 ($\pm$0.0813) when uncertainty in the survival parameters is included.

Perturbations - effect of additional mortality

To determine the effect of additional mortality on the growth rate, we analysed the model in the same way. However, this time we considered different scenarios. We looked at additional mortality rates of 1%, 5%, and 10% for both age stages. This was done by subtracting the additional mortality from the mean survival. The resulting growth rates are plotted in figure 3.10. The median population growth is nearly 1 (i.e. a stable population) with an additional mortality of only 1%. The population declines at 5% and 10% additional mortality.

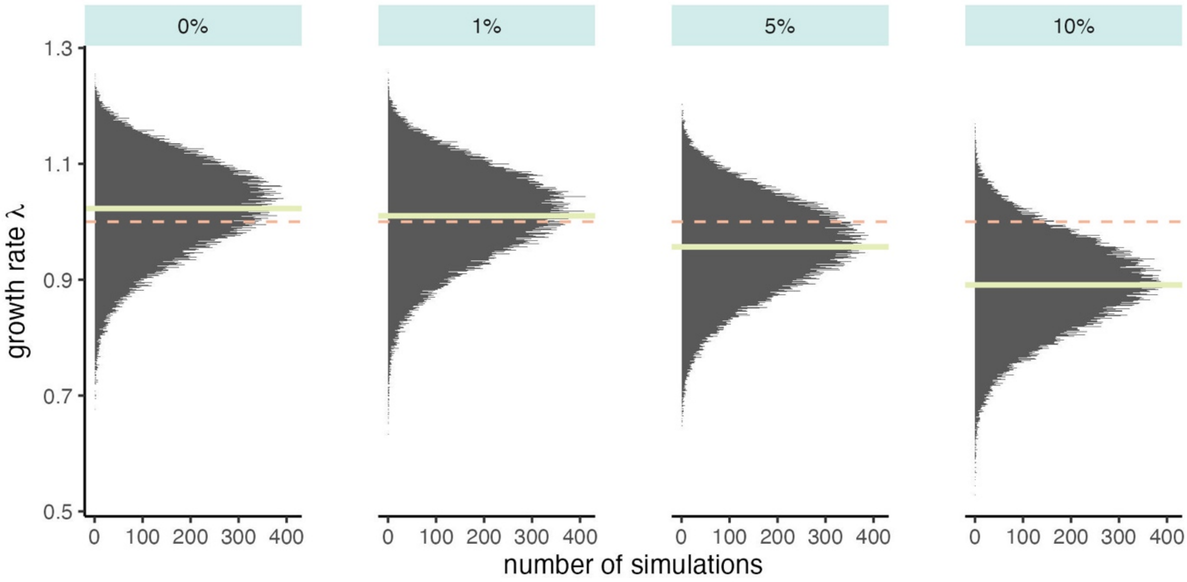

Figure 3.10. Growth rate of Eptesicus serotinus under different additional mortalities of 0% to 10%. Shown are the resulting growth rates λ from 10.000 simulations for each scenario. Green line: mean growth rates. Dashed red line: population growth 1, i.e. stable population.

Table 3.11. Monte Carlo simulation mean, s.e. and 25 and 75% quantiles of the growth rates λ under different additional mortalities of 0% to 10% for Eptesicus serotinus.

Scenario	mean	MC s.e.	Q25	Q75
0%	1.0229	0.08138	0.8494	1.166
1%	1.0102	0.08086	0.8388	1.153
5%	0.9566	0.08104	0.7868	1.104
10%	0.8909	0.08067	0.7260	1.041

Foto: Wesley Overman

NYCTALUS NOCTULA

Parameters and model structure

To parameterise the population model for *Nyctalus noctula*, we had two sources available. Heise (1989) uses life tables to estimate survival for juveniles and adult females in breeding colonies in Uckermark over 3 years. Korner & Nagy (2018) recalculated these values and gave confidence intervals for these values. We recalculated these to standard-deviations, arriving at the values given in the table below. Steffens et al. (2004) also analysed survival data but does not report annual survival rates.

Average litter size given by Gaisler et al. (1979; in Haarsma & Siepel 2003) as 1.8 juveniles per female, by Heise (1989) and Heise & Blohm (2003) as 1.48 juveniles per female (with a "range" of 1.26-1.82). We select the latter for the model as this paper also gives raw data per year per roost given and because the fraction of non-reproducing females in the colony is included in calculations.

The available parameters allowed us to formulate a model with juvenile and adult females (figure 3.3), with uncertainty in the survival rates. This means that, assuming an equal sex ration, the litter size for the model becomes 1.48 divided by 2 for number the female offspring per adult female. Heise (1989) reports a fraction of 0.98 reproducing females in the studies breeding colonies.

Table 3.12. Vital rates of Nyctalus noctula *adult females and juvenile females used in the population model.*

Parameter	Age/stage	Value (s.e.)	Source
Fraction reproducing	Females	0.98	Heise (1989)
litter size (b)	Females per female	0.73	Heise (1989)
Survival	Juvenile females	0.657 (0.0957)	Heise (1989) in Korner & Nagy (2018)
Survival	Adult females	0.574 (0.0280)	Heise (1989) in Korner & Nagy (2018)

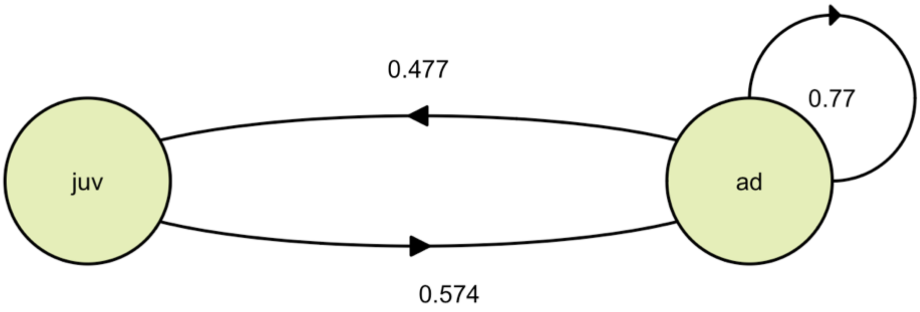

Figure 3.11 The model structure for Nyctalus noctula*.*
Only the females of the population are modelled.

Model analysis and projection

The approach is similar to the previous two species.

First, we analysed the static Leslie model the classical way. Growth rate λ is 0.883, so the simulated population is declining. The sensitivity analysis shows that the model is most sensitive to changes in adult survival with an elasticity of 0.481 for adult survival, and 0.259 for both juvenile survival and reproduction.

Next, we included parameter uncertainty by generating survival rates from a Beta distribution with the means and standard deviations in the table above. These generated survival rates were plugged into the model, and using this model we calculated the growth rate, sensitivity of the growth rate to juvenile and adult survival rate changes for those parameter values. We did this 10.000 times, each time with newly generated parameter values. The results of this Monte Carlo simulation were then summarized and plotted as frequency plots (figure 3.12). The model, parameterised with German field data, shows a population growth rate λ of 0.882 (±0.0468) when uncertainty in the survival parameters is taken into account. In other words, the parameter values we derived from literature are most probably those of an already declining population. This is in line with the Red List of Mammals of Germany (Meinig et al. 2020), that lists N. noctula as Endangered ("gefährdet") or critically endangered ("stark gefährdet") in a number of Federal states of Germany.

Perturbations - effect of additional mortality

To determine the effect of additional mortality on the growth rate, we ran 4 different scenarios. Apart from the model without additional mortality, we looked at additional mortality rates of 1%, 5%, and 10% for both age stages. This was done by subtracting the additional mortality from the mean survival.

The resulting growth rates are plotted in figure 3.12. The population declines more strongly as additional mortality increases.

Table 3.13. Monte Carlo simulation mean, s.e. and 25 and 75% quantiles of the growth rates λ under different additional mortalities of 0% to 10% for Nyctalus noctula.

Scenario	mean	MC s.e.	Q25	Q75
0%	0.8824	0.04681	0.7877	0.9710
1%	0.8675	0.04654	0.7736	0.9559
5%	0.8080	0.04655	0.7148	0.8971
10%	0.7336	0.04629	0.6412	0.8228

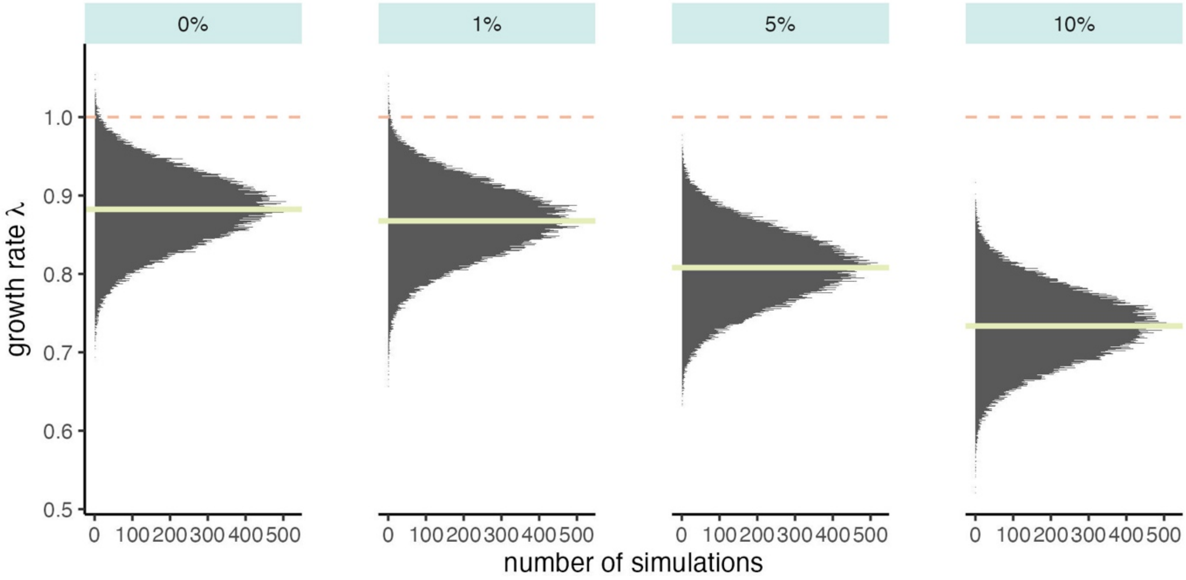

Figure 3.12. Growth rate of Nyctalus noctula *under different additional mortalities of 0% to 10%. Shown are the resulting growth rates λ from 10.000 simulations for each scenario. Green line: mean growth rates. Dashed red line: population growth 1, i.e. stable population.*

Foto: Joris Verhees

NYCTALUS LEISLERI

Parameters and model structure

For parameterising the model for *Nyctalus leisleri*, we used the data from a ringing study in Wassungen (Germany) by Schorcht et al. (2009). Schorcht et al. (2009) published annual survival rates with confidence intervals for males and females in classes of first year, second year and third year and over. The apparent survival rate for first year males is extremely low. The authors indicate that this may be a large overestimation, as juvenile males tend to not return to the breeding roost or birth site in the first year but disperse. For this reason, we assume that the survival rate for 1st year males is similar to first year females.

For number of young per female, we use the value of 1.73 from Lenteni et al. (2015). We assume that this figure encapsules the fraction of females reproducing. Sources about the age of first reproduction are scarce, but Schmidt (2010.) reports reproduction in the first year. We implement reproduction in stages 2 and 3 (in the second and third year of life) and assume that litter sizes are similar for both female life stages.

Using these parameters (table 3.14), we formulate a model with 6 stages: males and females in three age classes (figure 3.13).

Table 3.14 Vital rates of Nyctalus leisleri *used in the population model.*

Parameter	Age/stage	Value	Source
fraction reproducing	adult female	-	unknown
litter size		1.73	Lentini et al., 2015
survival rate	female 1st year	0.454 (0.037)	Schorcht et al., 2009.
survival rate	female 2n year	0.728 (0.045)	Schorcht et al., 2009.
survival rate	female 3rd year	0.756 (0.042)	Schorcht et al., 2009.
survival rate - reported	male 1st year	0.042 (0.076)	Schorcht et al., 2009.
survival rate- used (see text)	male 1st year	0.450 (0.037)	Schorcht et al., 2009.
survival rate - r	male 2n year	0.554 (0.199)	Schorcht et al., 2009.
survival rate	male 3+ year	0.690 (0.072)	Schorcht et al., 2009.

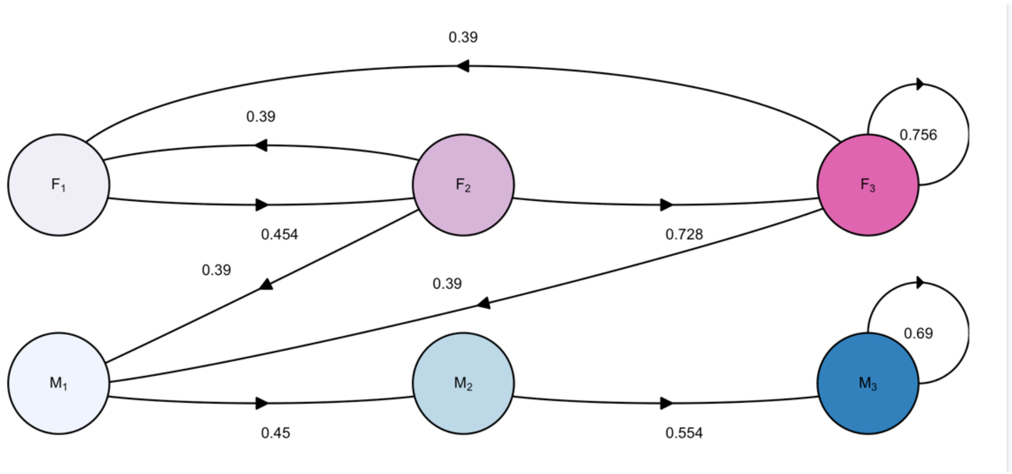

Figure 3.13 The model structure for Nyctalus leisleri.

Model analysis and projection

The approach is similar to the previous three species. First, we analysed the static Leslie model the classical way. Growth rate λ is 1.030. The sensitivity analysis shows that the model is most sensitive to changes in survival of females of three years and older (elasticity of 0.424).

Next, we included parameter uncertainty by generating survival rates from a Beta distribution with the means and standard deviations in the table above. Using these, we calculated the growth rate, sensitivity of the growth rate to juvenile and adult survival rate changes for those parameter values. We did this 10.000 times, each time with newly generated parameter values. The results of this Monte Carlo simulation were then summarized and plotted as frequency plots (figure 3.14). The model shows a population growth rate λ of 1.031 (±0.0360) when uncertainty in the survival parameters is considered.

Perturbations - effect of additional mortality

To determine the effect of additional mortality on the growth rate, we ran 4 different scenarios. Apart from the model without additional mortality, we looked at additional mortality rates of 1%, 5%, and 10% for both age stages. This was done by subtracting the additional mortality from the mean survival rates in the model.

The resulting growth rates are plotted in figure 3.15. Between 1% and 5% additional mortality, the mean growth rate drops below 1 and the population declines.

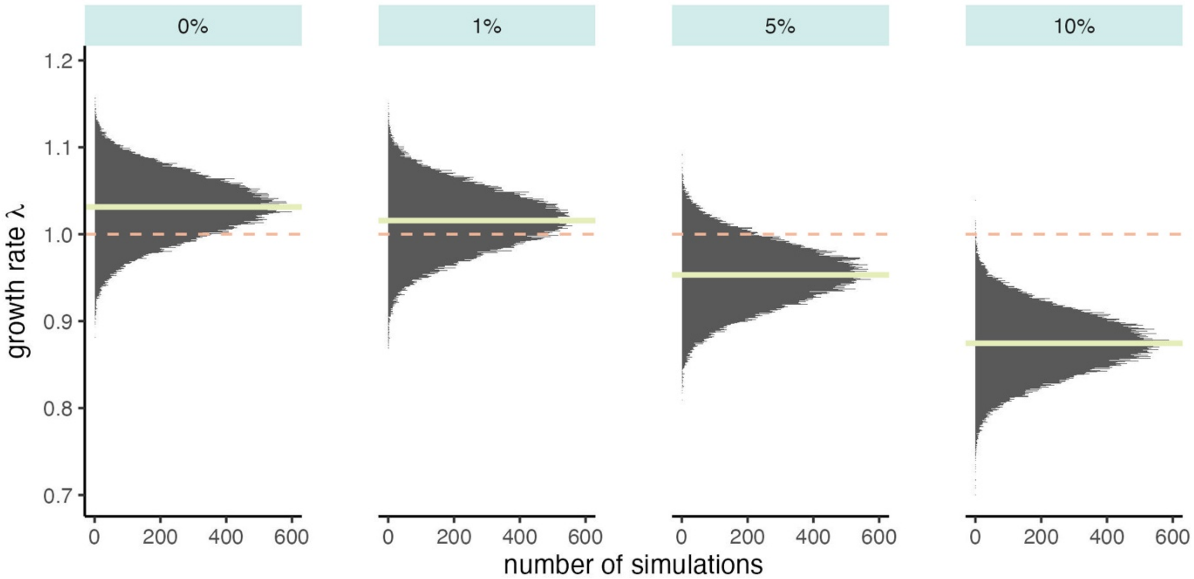

Figure 3.14. Growth rate of Nyctalus leisleri *under different additional mortalities of 0% to 10%. Shown are the resulting growth rates λ from 10.000 simulations for each scenario. Green line: mean growth rates. Dashed red line: population growth 1, i.e. stable population.*

Table 3.15. Monte Carlo simulation mean, s.e. and 25 and 75% quantiles of the growth rates λ under additional mortalities of 0%, 1%, 5% and 10% for Nyctalus leisleri*.*

Additional mortality	mean	MC s.e.	Q25	Q75
0%	1.0313	0.03596	0.9587	1.0995
1%	1.0157	0.03600	0.9439	1.0845
5%	0.9532	0.03604	0.8811	1.0222
10%	0.8746	0.03630	0.8027	0.9447

OVERVIEW OF PERTURBATION ANALYSES

We modelled the population dynamics of 6 of the 7 study species, using values for vital rates from the scientific literature. The resulting population models show that the populations without additional mortality grow moderately to slowly, but the population model of N. noctula predicts a decline (table 3.16; figure 3.15). The models of all species slow a decline at 10% additional mortality. Different additional growth rates had different effects depending on the species (and its vital rates). Some species are stronger affected by additional mortality than others: P. *nathusii*, N. *leisleri* are most sensitive to additional mortality, as can be seen by the steeper decline in the growth rate. The additional mortality value where the population changes from growing to declining differs per species.

Table 3.16. Overview of growth rates without additional mortality and with additional mortality of 1%, 5% and 10%.

Species	0%	1%	5%	10%	Enters decline between
Pipistrellus pygmaeus	-	-	-	-	-
Vespertilio murinus	1.0960	1.0810	1.021	0.9500	5 and 10%
Pipistrellus nathusii	1.0620	1.046	0.9825	0.9024	1 and 5%
Pipistrellus pipistrellus	1.1172	1.1018	1.0392	0.9606	5 and 10%
Eptesicus serotinus	1.0229	1.0102	0.9566	0.8909	1 and 5%
Nyctalus noctula	0.8824	0.8675	0.8080	0.7336	already in decline
Nyctalus leisleri	1.0313	1.0157	0.9532	0.8746	1 and 5%

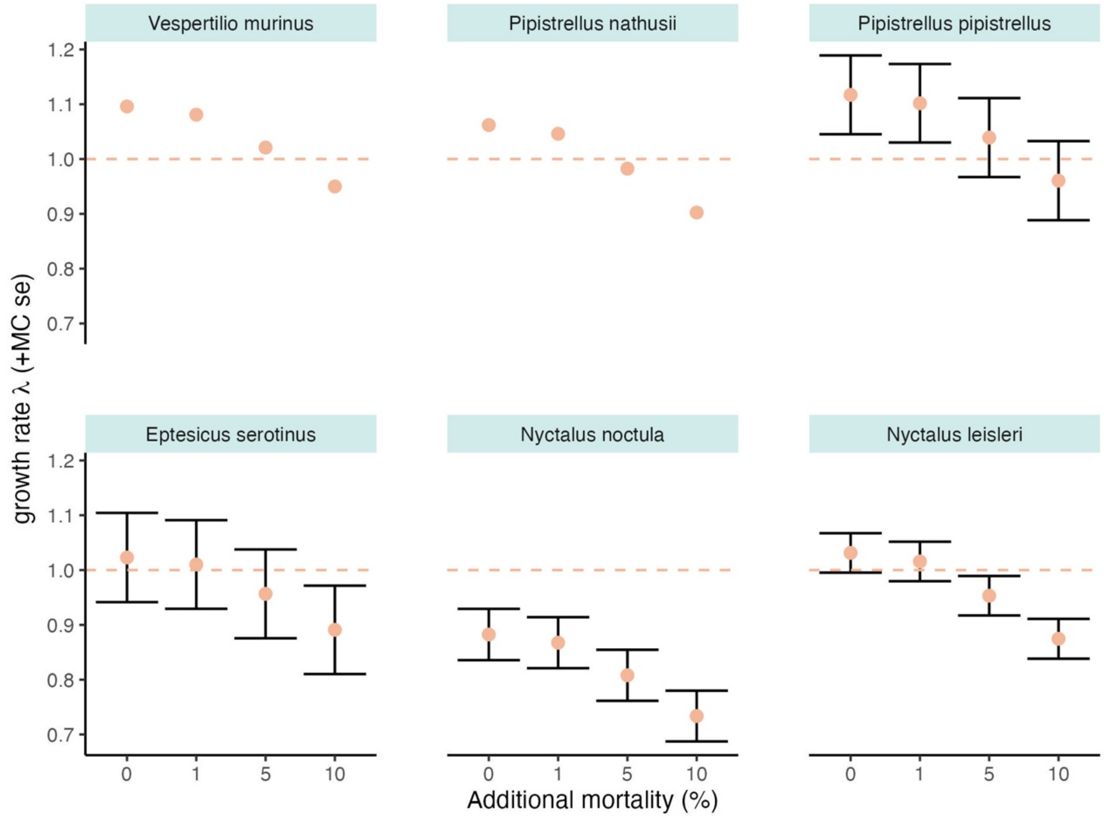

Figure 3.15. Growth rate (with Monte-Carlo standard errors, when available) for models with no additional mortality and 1%, 5% and 10% additional mortality for Vespertilio murinus, Pipistrellus nathusii, P. pipistrellus, Eptesicus serotinus, Nyctalus noctula and Nyctalus leisleri.

Table3.17: National trend ((± SE) in population size or occupancy of the study species (Schillemans et al., 2023). NEM-VTT = Dutch Network Ecological Monitoring – Car based Bat Transect Counts

	Population-trend NEM-VTT 2023			Output NEM-VTT
Pipistrellus pygmaeus	No	-	-	Occurrence
Vespertilio murinus	No	-	-	Occurrence
Pipistrellus nathusii	Yes	0.997 (±0.0092)	Stable	Occurrence + Trend
Pipistrellus pipistrellus	Yes	1.028 (±0.0075)	Moderate increase	Occurrence + Trend
Eptesicus serotinus	Yes	0.984 (±0.0063)	Moderate decline	Occurrence + Trend
Nyctalus noctula	Yes	1.034 (±0.0081)	Moderate increase	Occurrence + Trend
Nyctalus leisleri	No	-	-	Occurrence

OVERVIEW OF ELASTICITY ANALYSES

For each of the models (without additional mortality) a sensitivity analysis was done. The sensitivity of a parameter quantifies how changes in the parameter change the growth rate. A high sensitivity value for a parameter means that even a small change in that parameter will have a large impact on the growth rate λ. Sensitivities can be scaled to indicating how a 1% change in a parameter affects λ by percentage. This is called elasticity and allows comparison between different types of parameters (change in survival versus change in litter size) and comparisons between models.

In all models, the growth rate was most sensitive in absolute and relative terms to changes in the survival of female adults (table 3.18a and b). In absolute sense, reproduction was the second strongest factor and not the survival of juveniles to adulthood. However, the elasticities indicate that the effects were equally strong.

Table 3.18a Sensitivities (S) and elasticities (E) of the parameter values are given for each model. Only values for observed transitions are given null values are omitted.

Species		Survival adult female	Survival juvenile	Reproduction
Vespertilio murinus	S	0.765	0.338	0.530
	E	0.530	0.235	0.235
Pipistrellus nathusii	S	0.750	0.375	0.500
	E	0.500	0.250	0.250
Pipistrellus pipistrellus	S	0.778	0.311	0.555
	E	0.555	0.222	0.222
Eptesicus serotinus	S	0.801	0.264	0.602
	E	0.602	0.199	0.199
Nyctalus noctula	S	0.741	0.399	0.481
	E	0.481	0.259	0.259

Table 3.18b Sensitivity and elasticity of the parameters in the model for N. leisleri.

Transition		Sensitivity	Elasticity
Reproduction	female 2n year	0.093	0.056
	female 3+ year	0.254	0.155
Survival rate	female 1st year	0.479	0.211
	female 2n year	0.219	0.154
	female 3+ year	0.578	0.424

4. DISCUSSION

PARAMETERS TO BE IMPROVED

In 2018, Behr *et al*. explored the potential of using population models for estimating the effect of wind turbine mortality on bat populations in Germany, and the parameters required for such models, and concluded that the required data on the demography of relevant bat species is not available. Since then, more data have become available, but modelling the population dynamics, even in this simple approach, required pooling parameters from different studies in different habitats and regions in Europe.

The major difficulty in any demographic study still is a scarcity in required baseline data, fecundity (litter x percentage of females reproducing) and stage-sex specific survival rates. We found no values from studies performed in the Netherlands. Looking at the species in our study, a little reported species is *Pipistrellus pygmaeus*. We did not find (apparent) annual survival rates for juveniles.

The sensitivity analyses of each of the population models show that the parameter with the most impact on the predicted growth rate is adult survival. This is in line with modern theory on life history ecology (Stearns, 1994). As this is the most impactful part of the population dynamics, this is also the parameter which most urgently needs improvement and assessment of data from the Dutch population(s).

Litter size and fraction reproducing females

When litter size is reported, it is rarely made explicit whether the authors report the number of young per female, average litter size or fecundity. But these are very different values and certainly not the same. The litter size or number of young per female is just that. Often reported almost qualitatively, "the species usually has 2 young", this is an average number of offspring of females *that are reproducing*. This does not take into consideration the fact not all adult females may reproduce each year (Barclay et al., 2004).

An important factor in calculating fecundity is the fraction of adult females that reproduce. We found four sources that reported this or included this in the average number of young per female.

No study we could find reports uncertainty or natural variation in number of offspring.

Actual versus apparent survival rate

It is important to realise that many of the analyses and studies cannot separate between survival and emigration. Often, the data stem from annual mark-recapture studies, where survival is calculated from animals that are marked and then caught again in the year later. Modern analytical methods can separate survival and detection probability, but such 'live encounter' data again cannot inform the researcher whether animals are not caught because they have died or because they have emigrated out of the study area (Armstrup et al. 2005). Often therefore the term "apparent survival rate" is used. This issue is most apparent in studies on species where females and male do not roost or where males are the main dispersers. Here, estimated survival rates have low recaptures and large confidence intervals. The issue is most pronounced in small scale live encounter studies, and mostly negligible in regional or national large scale ringing studies, especially if enough (dead) ringed animals are re-encountered, or when there are enough observations to calculate migrations between metapopulations (Armstrup et al., 2005; Cooch & White, 2023).

Steffens et al. (2004) analyse a great (in quality and quantity) dataset of bat ringing data. However, they report estimated mean age of the population of and do not report annual survival. In our view this great dataset merits an analysis using modern mark-recapture analyses to calculate annual survival rates needed for population models.

Although we are uncertain about the exact growth rate, it is clear that additional mortality systematically hinders the population. In other words: the models are fairly precise but not necessarily accurate *yet*: the trend of the effect of additional mortality is clear but the exact growth rate is not. So, whether additional mortality will cause a population to shift from growing or stable to declining can only be known when better knowledge on vital rates is generated.

FROM POPULATIONS TO INDIVIDUALS

A challenge remains connecting individual bats killed at wind turbines and the likely location of their local populations, particularly for migratory bats (Voigt *et al.* 2012, Lehnert *et al.* 2014). An ecologist can estimate the number of victims per turbine, by extrapolation or systematic victim monitoring. So, for additional mortality we have an absolute number of victims per year.

However, for 'natural' mortality rates, we rely on mark-recapture data which result in fractions/percentages per year. So how do we convert the additional mortality in percentages to an actual victim number in individuals per year? Can we estimate the population size and assume mortality fractions to estimate the number of animals dying naturally?

Even when such demographic parameters have been established for local bat populations over many years, it is difficult to distinguish between effects caused by wind turbines and those triggered by other confounding factors, such as changes in the management of local habitats, losses of daytime roosts, annual climatic fluctuations (e.g. increased winter mortality caused by a sequence of harsh winters) and global climate changes.

May *et al.* (2019) discusses how choices in methodology of scaling up from individuals to the population level affect the estimates and warns that even robust monitoring and advanced modelling might not capture the complex effects of wind turbines on wildlife.

RECENT AND FUTURE MODELLING WORK

More recently, Diffendorfer *et al.* (2017) present a broader methodology to assess population-level effects of wind energy facilities, using ecological knowledge, demographic models and the potential biological removal concept. Again, the authors stress that the data required to make the assessment may be currently lacking or is of insufficient quality for some species. There is also tool to make modelling easier for the less mathematical inclined ecologist: Wiens et al. (2023) constructed an R statistics package to facilitate building and running age-structured population models ('Leslie matrices') specifically aimed at modelling bat populations, with an easy user interface. They demonstrate the modelling approach by giving a working example of effects of wind turbines for four US bat species. But again, better parameters are needed.

It is important to realise that population models can be used for fundamental scientific purposes, but here are used to help in policy and management. To apply models effectively, Cochrane gives a 11 rules and caveats for modelling for nature conservation policy (Table 4.1).

Table 4.1 Rules and caveats of pragmatic modelling to support management planning. Source: Cochrane et al., 2003.

Rules	Caveats
1. Work as a team with modelers, biologists, and managers	Requires full commitment and good communication skills Continually reaffirm common understanding of objectives and methods
2. The problem must be well defined *first*	Begin from a system or big-picture perspective rather than from the components
3. The purpose of pragmatic modelling is to gain insights and improve management decisions, not to produce precise predictions or absolute answers	Stochastic modelling is well suited to strategic planning (such as setting priorities for regional endangered-species recovery) but is not a panacea for site- and case- specific risk assessments under high uncertainty
4. The project and models must be flexible and adaptable	Be able to change directions (including redirecting funding)
5. Use rapid prototyping and iterative modelling with re-evaluation of objectives and process	Rapid turnover of preliminary results to management engages managers in the project and promotes continual focus on modelling relevance and iterative refinement of the objectives and approach Be willing to throw out models that are not working and start over
6 Models must be transparent or easily understood and manipulated	Be careful in using others' models
7. Avoid filing models with extraneous details; err toward simplicity and transparency	Details or variations can always be added if they become important to the objectives
8. Balance what is clearly known with what must be hypothesized	Avoid concentrating on what is already known while ignoring elements that are relevant to the objectives but poorly understood
9. Choose the model scale carefully, build more than one model at different scales	Generally, scales cannot be blended, if needed match objectives
10. If a simple model does not meet the work consider using a suite of models (each with a well-defined objective)	All-purpose or comprehensive models do not work Modelling experiments built around scenarios can reduce complexity while exploring a wide range of conditions and parameter values
11. Sensitivity analysis is essential	Be explicit about the assumptions and guesses that inevitably must be made to develop a model (virtual world) representation of the real world Sensitivity analysis tests these assumptions and provides essential perspective

CONCLUSIONS

In this modelling exercise, we formulated population models of 6 of the 7 study species, using values for vital rates from the scientific literature. However, these values stemmed from (sometimes very) different countries and habitats, and from good, but quite local studies. For one species, P. *pygmaeus*, we could not find the parameter values needed to model the population.

The resulting population models based on values for reproduction and mortality from the field, show that the populations grow moderately to slowly. However, the population model of N. *noctula* predicts a decline even at 0% additional mortality. The predictions are certain about the effect of additional mortality on bat populations, but because of the uncertainty in vital rates of the study species, the exact tipping points from growing or stable populations to declining population too are uncertain.

The models of all species show a declining population when there is 10% additional mortality. More specifically, *Vespertilio murinus* and *Pipistrellus pipistrellus* enter decline between 5 and 10% additional mortality, P. *nathusii*, *Eptesicus serotinus* and *Nyctalus leisleri* between 1 and 5%, and N. *noctula* is predicted to be already declining. Obviously, the tipping point, the additional mortality value where the population changes from growing to declining, differs per species.

Using a single rule of thumb for acceptable additional mortality (1, 5 or 10%, based on data from all over Europe) is a too simplified approach. To sustain populations of bats, additional mortality thresholds need to be calculated for local populations using local data.

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