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Long-term population trends of the lesser horseshoe bat *Rhinolophus hipposideros* and the greater mouse-eared bat *Myotis myotis* in Poland

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**ABSTRACT**

Bats are particularly susceptible to environmental changes because of their low reproductive rate, longevity, and high metabolic rates, which lead to relatively high food requirements. Thus, bat populations take a relatively long time to recover from increased mortality rates, and monitoring schemes should cover long time periods. In this work we analyzed the population trajectories of two bat species, *Rhinolophus hipposideros* and *Myotis myotis*, the most numerous in five caves in southern Poland, which are known as important bat hibernacula on a continental scale. Data were collected by regular counts in 1985–2001, depending on the particular cave; in addition, previous data on the number of hibernating bats in these caves, available since 1951, were taken from existing publications. We analyzed time-series data using average locality indices and TRIM methods, and both produced similar results. Generally, the populations of the two studied bat species showed recent increasing trends, especially visible as an effect of recovery after years of decline. The situation recorded in southern Poland is very similar to that described in other places in Europe, where recoveries of bat populations have also been observed in the last decades. Although it is difficult to present results from formal analyses, because of the lack of good data, at least some factors—less exposure to contaminants (pesticides, heavy metals), improving food availability due to climate change, and a lower predation rate (including human pressure), both in the breeding season and during wintering—positively affected both species.

**Introduction**

Bats are particularly susceptible to environmental changes because of their low reproductive rate, longevity, and high metabolic rates, which lead to relatively high food requirements. Thus, bat populations take a relatively long time to recover from increased mortality rates. Moreover, bat populations show responses to environmental stressors, ranging from alterations in habitat quality to climate change, as well as direct
exploitation\textsuperscript{4-6}, and bats are thus recognized as excellent indicators of anthropogenic changes in the environment\textsuperscript{7-9}.

Important for methodological, statistical and conservation purposes are the existing long-term series, coming mainly from winter bat censuses, especially in caves\textsuperscript{10,11}. For example, bats have been counted since 1944 in the Schenkgroeve, an artificial limestone cave in south Limburg in the Netherlands\textsuperscript{12}, since 1946 in Hermann’s cave in Lower Austria\textsuperscript{13}, and since 1957 in some caves in the Moravian Karst, Czech Republic\textsuperscript{14}. Thanks to the results obtained, it was discovered that European bat populations, particularly the lesser horseshoe bat *Rhinolophus hipposideros* and the greater mouse-eared bat *Myotis myotis*, declined dramatically in the second half of the 20th century\textsuperscript{15-18}. After the period of decline, since the 1990s bat populations have begun to recover\textsuperscript{19}. An increase in the number of some species of hibernating bats has been reported from many European countries: Austria\textsuperscript{13}, Belgium\textsuperscript{20}, the Czech Republic\textsuperscript{21,22}, the UK\textsuperscript{23}, Italy\textsuperscript{24}, Ireland\textsuperscript{25}, the Netherlands\textsuperscript{12}, Poland\textsuperscript{26}, Slovakia\textsuperscript{18}, Spain\textsuperscript{27}, Sweden\textsuperscript{28} and Switzerland\textsuperscript{17}.

The reasons for these changes in population trends have not been conclusively identified\textsuperscript{17,29-31}. It is believed that the bat population declines and subsequent increases may be caused by a combination of various factors, such as the spread of chemical pollutants, habitat destruction, changes in landscape structure, disturbance and destruction of roost sites, climate change, declines in insect prey, competition for prey, genetic inbreeding, and diseases\textsuperscript{17,19,32-34}.

Both species selected for this study, the lesser horseshoe bat *Rhinolophus hipposideros* (hereafter: RHH) and the greater mouse-eared bat *Myotis myotis* (MYM) have similar preferences for shelters. In winter both species hibernate in caves, mines and other cave-like structures. They prefer places with high humidity (over 80\%) and stable temperatures of 6–9 °C. In summer the females form maternity colonies in caves (Southern Europe) or in buildings with spacious roofs such as church attics and castles (Central Europe), where they give birth and nurse their offspring\textsuperscript{35-37}. Both species are insectivorous, but they differ slightly in their manner of foraging and their diet. RHH forages exclusively in woodlands, preferentially in dense areas, capturing its prey using echolocation in flight. It preys mainly on moths and Diptera. MYM preys on large, ground-dwelling arthropods such as beetles, crickets, and spiders, gleaning them from the ground\textsuperscript{38,39}. The two species are the most numerous hibernating species in the caves of
southern Poland, an important hibernaculum on a European scale\textsuperscript{11,16,40}. These species are excellent for monitoring population trends, as they are easy to recognize and are relatively easy to count, because they do not hide in crevices\textsuperscript{37,39}.

The aim of the study was to determine long-term population trends of the lesser horseshoe bat and the greater mouse-eared bat and the probable causes of changes in the numbers of hibernating bats of these two species.

**Results**

**Population size**

The detected number of individual bats between 1950 and 2020 was very variable. The lesser horseshoe bat reached its highest number in 2020 (the last year of observation). A total of 1050 individuals were found in the five studied caves. In four caves the highest number of individuals was observed in the years 2018–2020, although in the Racławicka cave the maximum was recorded in 1950. The greater mouse-eared bat reached its highest numbers in 2016: a total of 112 individuals were found in all five caves. In particular caves the maximum number of individuals was observed in the years 2009–2020.

**Analysis based on average locality indices**

For both species the $\beta$-coefficients for linear and quadratic functions were significant (Table 1). However, for both species a lack-of-fit test showed that a quadratic function was better than a linear one (Table 1). Calculation of the extreme point of the function for the lesser horseshoe bat showed that the population decreased up to the year 1979, after which it increased (Fig. 1). In the case of the greater mouse-eared bat, the extreme point occurred in 1980 (Fig. 1). We did not find any significant differences between the two values (chi-square = 0.98, $p = 0.86$).

| Bat species | Function | $\beta \pm SE$ | $p$ for $\beta$ | $R^2$ | Lack-of-fit |
|-------------|----------|----------------|----------------|--------|------------|
| RHH         | linear   | 0.041±0.0075   | <0.01          | 0.38   | F=299.5, $p<0.0001$ |
|             | quadratic| 0.0022±0.000014| <0.0001        | 0.89   |            |
| MYM         | linear   | 0.15±0.03      | <0.01          | 0.32   | F=243.8, $p<0.0001$ |
|             | quadratic| 0.0094±0.00055 | <0.0001        | 0.90   |            |

**Table 1.** Comparing the directional factor ($\beta$) for a population trends (RHH – lesser horseshoe bat, MYM – greater mouse-eared bat) between a linear and a quadratic function.
All of the tests showed the same slope for both species. RHH and MYM are stable and show a moderate increase. Models using the five caves as covariates have higher AIC, smaller Wald statistics and higher standard deviation than models without them (Table 2). The goodness-of-fit tests for both species are significant. The overall slope of the linear trend model for RHH and MYM represents a moderate increase. The indices show a sharp drop in the years 1950–1973; thereafter the indices are stable again until 2001. The early increase in 2002 was mainly driven by the population dynamics in the Ciemna and Wierzchowska caves. The imputed overall index for 2010 is equal to the index from 1951 (Fig. 2).

The overall slope of the linear trend model for MYM shows an increase (p < 0.01). The indices show a negative trend between 1951 and 1953, followed by a moderate increase to 1981. The first peak of the increase in 1991 is mainly driven by the population dynamics in the Nietoperzowa cave.

Despite the differences between the species, their numbers (expressed as a TRIM index of year-to-year changes) were moderately correlated (Fig. 3). We also found a positive relationship between the average annual temperature and the numerical change in the TRIM index for both species, while no such significant relationship was found for precipitation or the number of days with rainfall in a particular year (Fig. 3).
| Bat species | Covariates | AIC     | Wald-test covariates | Mean SE | Goodness-of-fit |
|-------------|------------|---------|----------------------|---------|-----------------|
| RHH         | Only time effect | 1724.6  | -                    | 0.093   | P<0.001         |
|             | 5 caves    | 1989.2  | 3.4, p = 0.48        | 0.459   | n.s             |
| MYM         | Only time effect | 297.7   | -                    | 0.113   | P < 0.001       |
|             | 5 caves    | 435.3   | 2.1, p = 0.57        | 0.243   | n.s             |

**Table 2.** Test statistics for the different TRIM models for RHH (the lesser horseshoe bat) and MYM (the greater mouse-eared bat).

**Figure 2.** Changes in relative abundance according to TRIM models for the lesser horseshoe bat (RHH) and the greater mouse-eared bat (MYM). Bottom part: DDT production in Poland and trends in heavy metal emissions.
Discussion

Both analytical methods produce similar results: a recent increase in population size, and an especially visible effect of recovery after years of decline. The situation is very similar to that described in other places in Europe, where recoveries of bat populations in the last decades have been reported. Below we discuss a set of potential factors that may have affected local bat populations, also paying attention to potential limitations in the explanation of population trajectories.

Exposure to organochlorine insecticides, especially DDT (dichlorodiphenyltrichloroethane), has been identified as a possible cause of declining bat populations. DDT was used ubiquitously for pest control in agriculture and forestry in Poland in the years 1946–1976, but since then the amount of DDT in the environment has been systematically decreasing. However, due to their relatively long lifetime and their high daily food intake, insectivorous bats may be exposed to higher concentrations of cumulative chemicals such as heavy metals, which accumulate through the food chain.

The caves studied are located between the Kraków agglomeration and the Upper Silesia industrial region, where there are hundreds of industrial facilities (metallurgical
works, chemical and cement plants, power stations). In the last decades of the 20th century, this region was the most polluted in Poland and one of the most polluted in Europe\textsuperscript{47}. As a result of the political and economic transformations in Poland at the end of the 1980s, industrial production, including that of heavy metals, declined considerably.

The area where the caves are located has not changed significantly since World War II. For both studied species the availability of woodlands (foraging areas) is crucial\textsuperscript{38,39}. However, the absence of significant changes in land use, particularly reduction in forest cover, indicates that changes in the physical (vertical) structure of habitats could not have been the main reason for the long-term changes in bat populations.

Both studied bat species (\textit{R. hipposideros} and \textit{M. myotis}) have similar preferences for winter and summer roosts\textsuperscript{37}. In winter, bats hibernate mostly in caves and other underground places. In the Polish Jura, the number of caves available for bats has not changed noticeably in the 20th and 21st centuries\textsuperscript{48}. In the caves we monitored, the conditions of hibernation have not changed since the early 1950s\textsuperscript{49}. The summer roosts in this area are not well recognized and have not been monitored. However, there is no information about a significant number of building renovations that might have caused the loss of summer bat colonies.

We found a significant positive correlation between the population trend of both species (RHH and MYM) and the average annual temperature in 1951–2020, but we did not find such a correlation with precipitation or with the number of days with rainfall in particular years (Fig. 3). Numerous earlier studies have demonstrated the impact of climatic conditions on the activity, survival, and reproductive success of bats\textsuperscript{50}. Climate influences food availability\textsuperscript{51,52}, timing of hibernation\textsuperscript{53,54}, frequency and duration of torpor\textsuperscript{55}, rate of energy expenditure\textsuperscript{33,36}, reproduction and the development rates of juveniles\textsuperscript{56-58}. Global warming may influence the species richness and distribution of bats\textsuperscript{59,60}. However, there are few studies showing the impact of temperature on bat population trends. Froidevaux, et al.\textsuperscript{29} found that the annual growth rate of maternity colonies of the greater horseshoe bat (\textit{Rhinolophus ferrumequinum}) in the United Kingdom was strongly correlated with spring temperatures and precipitation. Jones and Rebelo\textsuperscript{54} believed it highly likely that warmer conditions have contributed to considerable increases in abundance since 1997 for two species of horseshoe bats (\textit{R. ferrumequinum} and \textit{R. hipposideros}). Zahn, et al.\textsuperscript{33} compared the impact of severe
weather in Portugal and Germany on the body condition of *M. myotis*. They concluded that foraging constraints due to severe weather may contribute to poor body conditions, even when food resources are abundant. Thus, bouts of bad weather may cause high mortality in bats. On the other hand, Bowler, et al. emphasized that none of the temperature variables showed a significant relationship with long-term bat population trends. Mehr, et al. found that land use had a much greater effect than climate on bat species richness and community composition on a regional scale.

Our finding that long-term trends in bat populations were correlated with average annual temperature does not necessarily mean that temperature was the only factor affecting bat population changes. The correlation may be accidental, resulting from comparing two growing trends at the same time. Both studied bat species are thermophilic, which may be a reason for the effect of increasing temperature, and can benefit from warming. However, temperature does not explain the decreasing trends between 1950 and 1980. Bontadina, et al. also suggested that the fact that *R. hipposideros* was an abundant species early this century, when the climate was not significantly warmer than today, contradicts the scenario of a large thermic dependence as a single influencing factor.

We have no information on food availability for bats on a local scale. However, Przybyłowicz and Buszko observed that in the last few dozen years, the species richness of Lepidoptera in the Ojców National Park has decreased. On the other hand, monitoring of forest tree pests (insects) suggested that the most important insect pests have a tendency to outbreak in forests. In the vicinity of the study area the only tree pest whose numbers increased was the pine sawfly (*Acantholyda posticalis*), and in the years 1971–2018 the fluctuations in its numbers were very small. There is no information supporting the hypothesis that a shortage of insects could be the main cause of bat population changes. In Switzerland, Bontadina, et al. found that changes in prey abundance are unlikely to explain the demography of the lesser horseshoe bat. However, the same factors that affected bat numbers may also have affected the number of insects.

Bats have been considered to have a particularly effective immune system, but numerous bacteria and viruses apparently remain non-pathogenic in bats, likely due to a long process of co-evolution. Although bacterial, viral and parasitic infections may be among the main causes of bat deaths, no mass mortality from epidemics has been observed in Europe. There is very little information about bat diseases in Poland. No
mass mortality of bats or visible disease symptoms were observed in the caves of the Polish Jura during the winter censuses. We believe that diseases were not the main cause of long-term changes in bat numbers, but bats affected by other factors such as pollution may have been more susceptible to infection.

Temperate zone bats face a very low risk of predation. In particular, there are no predators specialized on bats in Europe. Owls are the only nocturnal predators that can prey on bats in flight, but this is a rare and opportunistic phenomenon, and only two species of European owls, the barn owl Tyto alba and the tawny owl Strix aluco, feed on bats more frequently. Occasionally, bats in roosts may be killed by domestic cats and martens. Predation is therefore a marginal factor with little impact on bat mortality.

On the other hand, the Ojców National Park is exposed to relatively high tourist pressure, due to its small area (2146 ha), attractiveness, and location close to the city of Kraków. This pressure can be estimated on the basis of the number of visitors to the Łokietka Cave, one of the Park’s greatest attractions. Sales of tickets to this cave have been recorded since 1960. There is no visible trend in the number of visitors. The current number of visitors (120 thousand in 2019) is close to the average for the whole period and to that of the early 1960s. The cave is only visited outside the bat hibernation season. Despite the high human pressure, no deliberate killing or disturbance of bats has been recorded in the caves of the Polish Jura.

Both studied species showed positive trends in population size over the long time period (1951–2020). Because the study has a correlational character, and because there was no access to detailed spatial and temporal environmental (and other) data, we discuss the main potential factors affecting both bat species according to the proposal of Bontadina, et al., and we rank their influence (Table 3).

| No. | Factor                                                   | Method of assessment       | Relevance of the assessment | Assessment of the importance of the factor |
|-----|----------------------------------------------------------|----------------------------|----------------------------|------------------------------------------|
| 1   | Exposure to contaminants (pesticides, heavy metals)     | data-based assessment      | high                       | +++                                      |
| 2   | Changes in the physical structure of habitats           | data-based assessment      | high                       | -                                        |
| 3   | Loss of roosts and roost deterioration                   | expert evaluation          | medium                     | -                                        |
| 4   | Climate changes                                         | statistical analysis       | high                       | ++                                       |
| 5   | Food shortage                                           | data-based assessment      | medium                     | +                                        |
| 6   | Competition against other species                        | expert evaluation          | medium                     | -                                        |
| 7   | Genetic inbreeding                                       | expert evaluation          | low                        | -                                        |
Table 3. Assessment of factors that may have caused changes in long-term population trends of the lesser horseshoe bat and the greater mouse-eared bat. List of factors after Bontadina, et al. 17. Factor assessment: “+++” – most important factor, “++” – might be important, “+” – might play some role, “-” – not relevant.

Conclusions

Both studied species, the lesser horseshoe bat and the greater mouse-eared bat, have shown a significant increase in wintering population size over the last 70 years. We noted two directions of change: until the 1980s the population of both species was decreasing, and after that time it was increasing. Similar trends have been observed throughout Europe19.

Although the search for factors affecting population size has only a correlative character, we must note that reduced exposure to contamination was probably the most important factor in the long-term changes in the populations of both of these bat species. However, other factors, including climate change, food shortage and diseases, may also play some role in changes in bat populations.

Material and methods

Study area

The five studied caves (Table 4) are located in the Kraków-Częstochowa Upland (also known as the Polish Jura) in the southern part of Poland (Fig. 4). The upland has elevations between 300 and 513 m a.s.l. The area is formed by upper Jurassic limestone, which creates a plate with single inselbergs several meters in height. This region is characterized by karst processes with numerous deep gorges, sinkholes, and caves73. Over 1800 caves and rock shelters of total length over 31 km are known in this area. Most of them are small: only 150 caves exceed a length of 40 m48. 20% of the region is covered by forests, dominated by deciduous and mixed types.

| No | Cave          | Length1 (m) | Relative height (m) | Altitude (m a.s.l.) | Protection |
|----|---------------|-------------|---------------------|---------------------|------------|
| 1  | Racławicka    | 165         | -26                 | 446                 | -          |
| 2  | Nietoperzowa  | 337         | -23                 | 447                 | G          |
Table 4. Characteristics of the studied caves (NP – cave located in the national park, G – gate at the entrance).

|   | Location         | Bats | Change | Total | Location |
|---|------------------|------|--------|-------|----------|
| 3 | Łokietka         | 320  | -7     | 453   | NP, G    |
| 4 | Ciemna           | 209  | +10    | 372   | NP, G    |
| 5 | Wierzchowska Górna | 975  | -25    | 390   | G        |

Figure 4. Location of the studied caves: 1 – Racławicka, 2 – Nietoperzowa, 3 – Łokietka, 4 – Ciemna, and 5 – Wierzchowska Górna (source of spatial data: OpenStreetMap.org).

Data collection

Standardized and regular annual censuses during the hibernation period (in the first half of February) have been conducted in the caves since 1985 (Nietoperzowa and Ciemna), 1991 (Łokietka), 2000 (Racławicka) and 2001 (Wierzchowska Górna). All bats roosting in the caves are counted. The counting protocol includes visual species determination and counts of visible hibernating bats with the aid of torches and binoculars. The persons who carried out winter bat censuses had required permissions from the Minister of Environmental Protection and the Ojców National Park Director. The last permission number is DOP-WPN.436.288.2019.MŚ. Previous data on the number of hibernating bats in these caves, available from 1951, were taken from existing publications40,49,74-77.
Climate data for the years 1951–2019—average annual temperature (°C), total precipitation (mm), number of days with rainfall—were obtained from the nearest meteorological station in Kraków (20 km to the south).

**Data analysis**

**Average locality index (ALI)**

Following Loman and Andersson \(^78\) and Kyek, et al. \(^79\) we calculated the average locality index (ALI), which allowed us to compare the average population changes of the two bat species over the years, even though the numbers of both species are very different. In the first step we calculated a locality index for each cave (\(LI_{ys}\)) using the formula

\[
LI_{ys} = \frac{N_{ys}}{\bar{N}_s}
\]

where:

- \(N_{ys}\) is the number of individuals counted for each species, cave and year
- \(\bar{N}_s\) is the average number counted for a particular species at a given cave

Values below 1 indicated a relatively low count of individuals, while numbers above 1 indicated a relatively high count. Then we calculated the average locality index (\(ALI_y\)) in all caves for each year, using the formula

\[
ALI = \bar{LI}_{ys}
\]

which represents the overall population trend for both species. Finally, we adjusted the linear and nonlinear trend of population change over time and tested the significance of Beta coefficients using a t-test.

In the case of monotonic functions, such as a quadratic function,

\[
f(x) = ax^2 + bx + C
\]

for each species we calculated an extreme point of the function according to the equation

\[
E = -\frac{b}{2a}
\]

which shows up to which year the population decreased in number, and analogously, from which year the number of individuals increased.

**TRIM**

The ALI method does not provide test statistics significant for population change, nor does it provide standard errors and 95% confidence limits. Thus, as a second approach to
analysis of the population trends we used TRIM (TRends & Indices for Monitoring data method)\textsuperscript{80}, implemented in the rtrim library for R. This procedure makes better use of the available data, especially when some data for the years are absent—a common issue in long-term time series (in our case in the years 1950–1980)—calculating standard errors and confidence limits and offering various test statistics; it also takes into account overdispersion and serial correlation of data\textsuperscript{80}. TRIM is also capable of categorizing data by covariates and testing their influence on the observed changes, using Wald tests.

TRIM fits log-linear models and indices that represent the effect of change between years, which indicates the relative variation of the total population size. Two types of indices are estimated: (i) model-based indices, which are the values predicted by the model; and (ii) imputed indices, which equal the observed count if an observation is made, and the model prediction for missing counts\textsuperscript{80}. Dissimilarity between the two indices reflects a mismatch between observed (i.e. imputed indices) and model predictions (i.e. model-based indices) and, therefore, a lack of fit of the statistical model applied. In the next step indices are used to estimate a mean annual change rate\textsuperscript{80}. This technique has been widely employed for the analysis of temporal series in bird populations\textsuperscript{81-83} and also bat populations\textsuperscript{18,19,24,27,29}. We developed models with and without covariates (five caves). The best-fit models were selected according to goodness-of-fit tests (the Likelihood Ratio (LR) and Chi-squared tests) and the Akaike information criterion (AIC). A significance value for a model greater than 0.05 indicates that the data fit a Poisson distribution and, therefore, that the model can be accepted. Indices, overall slope and Wald tests remain reliable in case of lack of fit\textsuperscript{80}. In case of overdispersion or serial correlation (default TRIM thresholds: > 3.0 and > 0.4 respectively) the Wald test for the significance of slope was employed\textsuperscript{80}.

All calculations were performed in the language R 4.0.2 using the stats, rtrim, psych and ggcorrplot libraries\textsuperscript{84}.

**Data accessibility**

Dataset available on request.
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**Additional Information**

**Competing Interests:** The authors declare that they have no competing interests.
Figures

Figure 1

Average locality index (ALI) with quadratic regression for the lesser horseshoe bat (RHH) and the greater mouse-eared bat (MYM).
Changes in relative abundance according to TRIM models for the lesser horseshoe bat (RHH) and the greater mouse-eared bat (MYM). Bottom part: DDT production in Poland and trends in heavy metal emissions.
Figure 3

Correlation matrix between the TRIM index of year-to-year changes in the number of bats for the lesser horseshoe bat (trim RHH) and the greater mouse-eared bat (trim MYM) and weather conditions: average annual temperature (Temp), total precipitation (Prec) and number of days with rainfall (DwP) in particular years.
Figure 4

Location of the studied caves: 1 – Racławicka, 2 – Nietoperzowa, 3 – Łokietka, 4 – Ciemna, and 5 – Wierzchowska Górna (source of spatial data: OpenStreetMap.org).