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Negative trend reversal after 16 years of constant growth: The case of *Rhinolophus hipposideros* in an Austrian mass hibernaculum (Chiroptera: Rhinolophidae)

Návrat negativního trendu po 16 letech stálého nárustu: případ *Rhinolophus hipposideros* v rakouském hromadném zimovišti (Chiroptera: Rhinolophidae)

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Abstract. The populations of bats hibernating in Hermann's Cave, Lower Austria, have been intensively studied for almost 160 years. Here we present the population trend of *Rhinolophus hipposideros* during the period 1985–2013. In contrast to wintering populations in nearby caves in Styria/Austria as well as in neighbouring countries (Czech Republic, Slovakia, Thuringia/Germany), we observed a statistically significant decline since 2007. Maximum numbers of *R. hipposideros* recorded in the cave were roughly the same (770–850 individuals) in 1856, 1945 and 2007. This indicates that despite environmental degradation which has occurred since 1856, the source area of the wintering population produced similar numbers of lesser horseshoe bats hibernating in Hermann's Cave as in the period when conditions were favourable.

Key words. Lesser horseshoe bat, population trends, hibernation, cave, Austria.

INTRODUCTION

Of the European bat species which declined markedly in the middle of the 20th century, the lesser horseshoe bat, *Rhinolophus hipposideros* suffered the most spectacular population crash (Feldmann 1967). Populations of continental north-western Europe have not yet recovered from the strong decreases and range contractions which started in the 1940s (Netherlands – van Vliet & Mostert 1997, Dekker et al. 2011; Luxembourg – Harbusch et al. 2002; Belgium – Verlinde 2003, Kervyn et al. 2009; Germany – Kock & Altmann 1994, Kulzer 2003, Zahn & Weiner 2004, Wissing 2007; Liechtenstein – Güttinger 2011; Switzerland – Bontadina et al. 2000).

In contrast, population trends in central Europe, viz. the eastern parts of Germany and the Czech Republic, Slovakia and Austria have developed positively after a decrease in the 1970s and 1980s. Local populations which had persisted in hills and uplands of Saxony, Saxony-Anhalt and Thuringia have experienced a constant increase in the 1990s after a low in the early 1980s (Zöphel et al. 2010); in underground sites of Moravia (Horáček 2010, Chytil & Gaisler 2012) an abundance drop in the 1970s was followed by an ongoing rise of abundance beginning around 1984; annual counts in 52 Slovakian hibernacula revealed a generally increasing

trend between 1992 and 2009 (Uhrin et al. 2010); and in Austria a long-term study (Sackl et al. 2011) demonstrated that the numbers of lesser horseshoe bats hibernating in Styrian caves had increased up to six times after a historical low in the 1970s and 1980s.

In this study, we report on results of a long-term study (1985–2013) of the population trend of *Rhinolophus hipposideros* hibernating in Hermann's cave in Lower Austria. This cave is one of the most important mass hibernacula of the lesser horseshoe bat in Austria. Its population of wintering lesser horseshoe bats has been known since 1856 (Kolenati 1857) and has been monitored since 1945/46 (Mrkos 1962, Baar et al. 1986).

MATERIAL AND METHODS

Study site

Hermann's Cave in Kirchberg am Wechsel (47° 37' N, 15° 58' E), Lower Austria, is located at the foothills at the eastern edge of the Alps. The hills consist of silicate bedrock with local inclusions of carbonate rocks in which extensive karst systems developed. The climate is characterised by an annual precipitation of 700–900 mm and an annual mean temperature of 8.3 °C.

Hermann's Cave is a maze-like system of mostly very narrow corridors and few large domes (maximum height 15 m) of 4.43 km passages-length and a vertical extension between 606 m and 679 m a. s. l. It is situated in a small marble lens with a base area of only 0.02 km². The altitude of the two entrances is 627 m and 670 m a. s. l., respectively (Hartmann & Hartmann 1997). A microclimate survey of Hermann's Cave was carried out during the years 1987 and 1991 (Mrkos 1993, Tiesner 1993, Skoda 1997). Temperatures were recorded using negative temperature coefficient sensors located at 25 points. Over the 5 year period, temperatures recorded between November and March ranged between −1.0 °C and +6.5 °C close to the entrance, and between 7.5 °C and 8.5 °C in the inner parts. In the warm season, when outside temperatures are higher than those in the cave, the cold air leaves the cave at the lower entrance and is replaced by warmer air. During the cold season, when ambient temperatures are lower than the cave temperatures, the cold air enters the cave at the upper entrance and remains in the cave.

With 17 recorded bat species, Hermann's Cave is the hibernaculum with the highest species diversity in Austria (Baar et al. 1986 and own observations). *Rhinolophus hipposideros* has been the dominant species of the hibernating bat community since at least 1856 (Kolenati 1857).

Hermann's Cave is one of the oldest show caves in Austria. In recent years, it has been visited annually by 30,000 persons between the end of March and beginning of November (Hartmann & Hartmann 1997, Mrkos 1997). The route taken by the visitors is 300 m long.

Hermann's Cave is legally protected and a Natura 2000 site under the EU Habitat's Directive.

Former (1942–1984) surveys and banding of hibernating bats

Winter surveys

Surveys of hibernating bats have been conducted continuously since 1945/46 (Mrkos 1962). Until 1984, bats hibernating along the route of the guided tour and in further 20 parts of the cave were counted. Not all censuses followed a regular strict protocol and thus produced inconsistent data which are not fully comparable to those obtained between 1985 and 2013.

Bat banding

A large-scale banding project of hibernating bats in Hermann's Cave started in 1942 (Vornatscher 1957). In 1971, marking of the lesser horseshoe bat was stopped, and in 1974 bat banding ceased completely. Between 1942 and 1974, altogether 6,838 bats were banded during hibernation. They belonged to 14 spe-

cies; the two most abundant species were *Rhinolophus hipposideros* (93.9%) and *Myotis myotis* (3.4%) (Mrkos 1997). The sex ratio of 6,145 lesser horseshoe bats banded until 1961 was 69% males and 31% females (Baar et. 1986).

Current census methods

Since 1985, standardised and regular annual censuses have been conducted at the beginning of the hibernation period in November ('autumn census', median date 16 November, range: Nov. 10–24) and at the end of the hibernation period in March ('spring census', median date 14 March, range: Mar. 6–31). We counted all bats roosting along the route of the guided tour, as well as in ten further chambers and corridors of the cave system. In total, the length of the surveyed tracks is approximately 700 m.

The counting protocol included visual species determination and counts of the visible hibernating bats with the aid of torches and binoculars. Bats were not handled, which precluded determination of sex, age and body mass.

As this method does not reveal the real numbers of vespertilionid bats hibernating in the cave (Roer & Roer 1965), and double infrared light barriers which automatically record the numbers of bats leaving and entering the cave (Kugelschafter & Lüders 1996, Gaisler & Chytil 2002, Berková & Zukal 2006) were not in use, we concentrated on *Rhinolophus hipposideros* as a study species. Apart from the greater horseshoe bat which occurs very rarely in Hermann's Cave, it is the only highly detectable bat hibernating in the cave. Counting lesser horseshoe bats produces reliable numbers of the complete colony size, as this species is unlikely to roost in the very narrow galleries which cannot not be visited by man (Issel 1950).

Statistical analysis

In a first step, we determined whether the results of the autumn counts differed significantly from the spring count in the same season. For this purpose, an intra-seasonal residual factor (*Re*) of both counts was calculated as $Re = \ln(Ns_t / Na_{t-1})$, where Na_t denotes the number of animals observed in autumn and Ns_t the number of animals observed in spring of the year t.

A significant deviation of *Re* from zero would indicate a significant difference between the counts in autumn and spring, respectively. Due to some missing data, *Re* could be calculated for 27 seasons (years 1985–1994 and 1996–2012) only. As a significant deviation of *Re* from zero was found ($t(26)=1.48$, $p=0.15$; estimated mean=−0.053), we decided to restrict the subsequent analysis to the more stable results of the autumn counts.

To model the evidently non linear temporal trend of the study population, we fitted – in accordance with the European bat monitoring guidelines (Battersby 2010) – a generalised additive model (GAM) with Poisson error structure and a cubic regression spline as implemented in the mgcv package (vers. 1.7-27; Wood 2013) to the untransformed count data. As an explaining variable we used the observation dates transformed into days after 1 January 1970. Cross-validation was used to optimize the model fit. The obtained model was validated by visually inspecting (1) the histogram of the model residuals for deviation from normality and (2) visible patterns in a plot of the model residuals vs. its fitted values which would indicate heteroscedascity.

All statistical analyses were conducted with R software (vers. 3.0.1; R Core Team 2013).

RESULTS

During our regular annual counts in the years 1985 to 2013, we recorded 26,526 specimens of lesser horseshoe bats: 13,403 during the autumn censuses and 13,113 during the spring censuses. The numbers of observed individuals per census ranged between 222 and 765 in autumn and between 176 and 707 in spring. The number of individuals observed during spring censuses

was on average 4 % lower than during the preceding autumn censuses. However, considerable variability in the difference, ranging from −40% to +34%, between individual numbers in autumn and the following spring was observed. Therefore we used only the results of the autumn counts for assessing the population trend.

After a steady increase between 1985 and 2001, the numbers of the lesser horseshoe bats hibernating in Hermann's Cave entered a period of pronounced fluctuation around c. 650 individuals with a maximum of 765 individuals during 2002 and 2007. In 2008, the population started to decline significantly to the current value of ca. 500 individuals (Fig. 1). The described population trend is supported by the significant smoother obtained from the GAM procedure (R^2=94.8%, $p<0.001$; edf.: 8.2; residual σ^2=1). Markedly increased inter-annual differences of individual numbers are apparent in the period between 2002 and 2013.

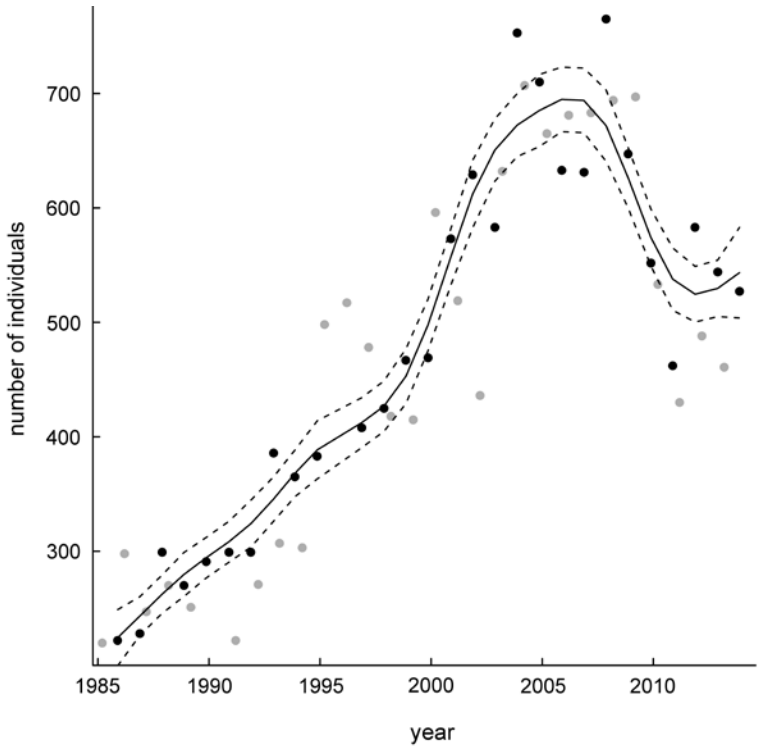

Fig. 1. Population development of *Rhinolophus hipposideros* in Hermann's Cave between 1985 and 2013. Black dots: numbers of individuals observed during autumn counts; grey dots: numbers observed during spring counts; solid line: fitted Poisson GAM smoother; broken line: 95% confidence intervals. The smoother is based on data from the autumn counts only.

Obr. 1. Vývoj populace *Rhinolophus hipposideros* v Hermannově jeskyni mezi roky 1985 a 2013. Černé body: počty jedinců pozorované během podzimních kontrol; šedé body: počty pozorované během jarních kontrol; souvislá čára: přizpůsobený vyhlazovač Poisson GAM; přerušovaná čára: 95% interval spolehlivosti. Vyhlazovač je založen pouze na údajích z podzimních kontrol.

DISCUSSION

Although the results of winter censuses before and after 1985 are not fully comparable, the maximum numbers of hibernating lesser horseshoe bats recorded in Hermann's Cave since 1856 can be considered as roughly similar: approximately 850 individuals in 1856 (Kolenati 1857), 880 in 1945 (Baar et al. 1986) and 765 in 2007 (this study). These observations support the statement of Lutsar et al. (2000) that the numbers of a particular species in a particular hibernaculum will continuously grow until they reach a certain maximum level. As Hermann's Cave does offer appropriate space for many more individuals than the recorded maxima, it can be assumed that the numbers of hibernating lesser horseshoe bats are determined by the numbers of bats migrating from their summer roosts to this cave. Recoveries of eight bats banded during hibernation in Hermann's Cave and found in central Burgenland and adjacent parts of Hungary (Mrkos 1962, Baar et al. 1986) indicate a maximum catchment area with a diameter of 50 km around the cave. In this context it is interesting to note that after almost 160 years of habitat impoverishment, this area was still able to produce roughly the same maximal numbers of lesser horseshoe bats.

The long series of records of lesser horseshoe bats hibernating in Hermann's Cave (Baar et al. 1986 and this study) reveals a decline of roughly 80% over 27 years (1945–1971) followed by a 10-year' phase of relative stability until 1982, and a period of continuous growth until the early 2000s. Similar population trends were observed in large parts of central Europe (e. g. Sackl et al. 2011, Tress et al. 2012, Horáček 2010, Uhrin et al. 2010, Anděra & Gaisler 2012, Bufka & Červený 2012, Chytil & Gaisler 2012). A recent trend reversal as observed in Hermann's Cave, however, has not yet been reported from anywhere else, but might be also indicated in Sackl et al. (2011) for a part of eastern Styria/Austria ("Weizer Bergland").

Whether the recent decline in the hibernating population of the lesser horseshoe bat refers to a local phenomenon typical for a subpopulation at the edge of the distribution area or is the first indication of a decrease in the numbers of *Rhinolophus hipposideros* in a wider range, can not yet be determined. However, results of our surveys confirm an ongoing decrease in Austrian maternity colonies for at least two decades. Until the mid 1990s, the lesser horseshoe bat was widely distributed in Austria (Spitzenberger 1997), missing only at altitudes above 1800 m a. s. l. and in the forest-free Pannonian plains. Already at that time, nationwide population trends in maternity colonies were negative (Spitzenberger 2002). More recently, results of two consecutive (1990–1997 and 2004–2008) surveys of potential bat roosts in buildings in Burgenland, from where the lesser horseshoe bats migrate to Hermann's Cave, demonstrated that this species had abandoned more than a half of formerly occupied roosts and lost 20% of adults in maternity roosts (Spitzenberger & Weiss 2012).

SOUHRN

Populace netopýrů zimujících v Hermannově jeskyni v Dolních Rakousích je intensivně studována posledních téměř 160 let. Zde je presentován trend populace vrápence malého (*Rhinolophus hipposideros*) zjištěný v posledním období (1985–2013). Narozdíl od situace populací vrápenců malých zimujících v jeskyních sousedního Štýrska (Rakousko), jakož i v sousedních zemích (Česko, Slovensko, Duryňsko v Německu), v Hermannově jeskyni byl pozorován statisticky významný pokles počtů od roku 2007 do současnosti. Nejvyšší počty *R. hipposideros* zaznamenané v jeskyni byly vždy obdobné (770–850 jedinců) a zjištěné v létech 1856, 1945 a 2007. To ukazuje, že navzdory úpadku životního prostředí, který je přítomen už od roku 1856, zdrojové území dotyčné populace produkuje podobné množství vrápenců malých zimujících v Hermannově jeskyni nyní, stejně jako v obdobích, kde byly podmínky příznivé.

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