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# Further evidence of large-scale population decline and range contraction of the little owl *Athene noctua* in Central Europe

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**Abstract.** Long-term population decline of the little owl has been recorded in Western Europe and available evidence also suggests severe range restriction in many Central European regions. Using two nationwide volunteer-based monitoring programmes during the years 2009–2016, we investigated distribution, population density and breeding associations of the little owl in the Czech Republic and Slovakia. Across the two countries combined, the average population density of the little owl was 0.19 calling males/10 km<sup>2</sup>. However, the population density was markedly higher in Slovakia (0.36 calling males/10 km<sup>2</sup>) than in the Czech Republic (0.09 calling males/10 km<sup>2</sup>). The overall breeding population of the little owl was estimated at 130 breeding pairs in the Czech Republic and 550 in Slovakia. Compared to the situation two decades ago, those estimates represented a 87–94 % decline in the breeding population in the Czech Republic and a 31–45 % reduction in Slovakia. Our data also revealed marked distributional range contraction of the little owl, indicating rapid local extinctions over the last two decades. The analysis of expected breeding places of the little owl confirmed a strong preference for man-made objects over the original breeding sites in tree cavities. In the light of our present results, we propose urgent preparation and implementation of a species action plan with conservation measures to halt the little owl's steep decline in Central Europe.

**Key words:** farmland birds, population trend, distribution, breeding places, agricultural buildings, conservation measures

## Introduction

Agricultural intensification has substantially affected populations of farmland birds, severely reducing farmland bird populations across Europe and diminishing their ranges (Fuller et al. 1995, Donald et al. 2006, Wretenberg et al. 2006, Reif et al. 2008). Population reductions have been robustly documented for a wide range of farmland species, including several once common and widespread farmland bird species. For example, populations of common farmland birds in Europe declined about 57 % in the period 1980–2013 (PECBMS 2015), leading to substantially reduced ranges and local extinctions (Fuller et al. 1995). Although the steepest declines in farmland birds populations have occurred in Western and Northern

Europe, long-term population declines have also been recorded in Central and Eastern European countries (Reif et al. 2008, Voříšek et al. 2010). Voříšek et al. (2010) have documented that, among farmland birds, residents and short-distance migrants have recorded steeper negative population trends than long-distance migrants. This suggests that marked changes in the agricultural landscape at breeding grounds and winter conditions are stronger drivers of population decline than conditions on wintering areas and migration routes. Avian farmland predators at the top of ecological food chain are considered to be important environmental indicators of habitat changes (e.g. Sergio et al. 2005, 2006) and may be particularly heavily influenced by agricultural intensification and habitat loss.

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The little owl (*Athene noctua*) is a residential farmland predator, widely distributed in a variety of semi-open habitats throughout Europe (van Nieuwenhuysse et al. 2008) but mainly connected with agricultural landscapes in Western and Central Europe (van Nieuwenhuysse et al. 2008, Šálek & Lövy 2012, Šálek et al. 2016). The species is classified as being of “least concern” in the European Red List (BirdLife International 2015) and some stable and growing populations have been identified across Europe (e.g. Kloibhofer & Lugmair 2012, Fiedler 2013, Kluschke 2013). Nevertheless, rapid population declines have been reported in several Western European countries during recent decades.

For example, the populations have decreased in Belgium, Germany, the Netherlands and the United Kingdom (van Nieuwenhuysse et al. 2008) and the species is near extinction in Denmark and Luxembourg (Lorge 2006, Thorup et al. 2010). Several local and national conservation programmes and management plans have been initiated to halt population declines (e.g. Vossmeier et al. 2007, van Nieuwenhuysse et al. 2008, Stange 2013, Sunde et al. 2015). However, even more alarming situation was reported in the Central European countries where steep large-scale population declines and local extinctions of the little owl have been identified (Ille & Grinschgl 2001, Vogrin 2001, Żmihorski et al. 2006, Kloibhofer & Lugmair 2012). In particular, a 50 % population decline was recorded in Poland between 1994 and 2004 (Grzywaczewski 2006, van Nieuwenhuysse et al. 2008, Kitowski & Stasiak 2013) and the current population is estimated to be 500-1000 breeding pairs (BirdLife International 2015). In Austria, the number of breeding pairs in 2010 declined to only 74, located in the north-eastern part of the country (Ille in Dobrý 2011). The little owl's population status in Hungary is generally insufficiently known, although some studies indicate stable population trends (Gorman 1995, BirdLife International 2015).

The present study explores the current status of the little owl in the Czech Republic and Slovakia, which differ markedly from each other in terms of the scientific evidence available on long-term changes in distribution and population parameters. More specifically, in the Czech Republic, robust evidence about changes in distribution and population density is known from three atlases of breeding bird distributions covering the period 1973-2003 (Šťastný et al. 1987, 1996, 2006) and three nationwide monitoring programmes in 1993-2006 (Schröpfer 1996, 2000, Šálek & Schröpfer 2008). Those studies indicate that the little owl's range shrank by about 60 % between

1985 and 2003 (Šťastný et al. 2006) and large-scale population density declined about 70 % between 1993 and 2006 (Schröpfer 1996, Šálek & Schröpfer 2008). Continuing population decline since the beginning of this century has been reported even from distribution centres where the little owl had reached relatively high population densities (Šálek 2014), inevitably leading to a highly fragmented population distribution within the country. In contrast to the Czech Republic, long-term trends in population size and distribution are generally poorly known in Slovakia. Pačeňovský (2002) characterised the little owl as widespread and a common breeder, facing slight long-term decline. However, local-scale studies indicate rapid population decline in recent decades (Šnirer et al. 2009, Dobrý 2011, Mojžiš & Kerestúr 2013, Václav 2016).

To gain a realistic overview of the current population status of the little owl in the Czech Republic and Slovakia, it is extremely important to assess its distribution and population trends. Detailed information on the distribution and breeding habits of the little owl is also crucial for nature conservation efforts as it enables conservation measures to be targeted at areas still inhabited by this rapidly declining species. Using volunteer-based nationwide monitoring programmes, we therefore examined the local and large-scale population densities and distribution to identify local distribution centres and total population sizes. We also investigated breeding preferences to identify the little owl's affinity to artificial and natural habitats.

## Material and Methods

The little owl's distribution and population density were monitored based on two nationwide volunteer-based programmes in the Czech Republic (CZ) and Slovakia (SK), Central Europe. The monitoring programmes were performed in the years 2015-2016 in the Czech Republic and 2009-2014 in Slovakia. The study areas were mostly distributed across lowland and highland farmland landscapes where the historical and current distributions of the little owl were predominantly situated (Pačeňovský 2002, Šťastný et al. 2006, Šálek & Schröpfer 2008) or where earlier studies of the species had been undertaken (Šálek & Schröpfer 2008, Šálek 2014). In total, the monitoring was performed in 55 study areas (30 in the Czech Republic and 25 in Slovakia) covering a total area of 17032.7 km<sup>2</sup> (10587.3 km<sup>2</sup> in the Czech Republic and 6445.4 km<sup>2</sup> in Slovakia). The average size of the study area was 309.7 km<sup>2</sup>, with a range from 19.5 km<sup>2</sup> to 1672 km<sup>2</sup> (Appendix 1). The borders

of individual study areas were determined based on landscape patterns and habitat composition or in accordance with the geographical location used in previous studies of the little owl (Šálek & Schröpfer 2008). The borders of study areas were defined by Voronoi Diagrams within Euclidean distance, which defines a cluster of surveyed points (surveyed points within villages) to the surrounding non-surveyed points (Aurenhammer 1991). Finally, the occurrence of the little owl was projected onto the  $12 \times 11.1$  km mapping squares grid used for atlases of breeding birds in the Czech Republic (Šťastný et al. 2006) and Slovakia (Pačeňovský 2002) to analyse changes in distribution in both countries. All analyses were performed in geographic information environment using ESRI and QGIS tools (ESRI 2014, QGIS Development Team 2014).

Monitoring of the little owl was based on a tape-recorded stimulation of the territorial voice, which is the most widespread method used for detecting the little owl's presence (van Nieuwenhuysse et al. 2008) and was successfully applied in previous nationwide programmes in Central Europe (Schröpfer 1996, 2000, Šálek & Schröpfer 2008). The methodology followed standard survey protocol for the little owl (Johnson et al. 2009), which is based on broadcasting a call sequence with the territorial voice lasting two

minutes and repeated three times. Each sequence was separated by a one-minute interval followed by a five-minute silent listening period (Clewley et al. 2016). The volume of broadcasts was adjusted to the sound pressure level of natural little owl calls (Jacobsen et al. 2013). Playback was immediately stopped when an individual responded. Since the recent distribution of the little owl in the Central Europe is closely associated with human-dominated landscapes (Šálek & Schröpfer 2008, Dobrý 2011, Šálek et al. 2013, 2016) the playback was mainly broadcasted within human settlements (e.g. agricultural and industrial buildings, old residential areas, edges of inhabited areas). However, several semi-natural habitats (e.g. parks, gardens, orchards, tree-lined avenues, vineyards, or pollard willow stands) were also monitored. The fieldwork was conducted from sunset to midnight during the survey period coinciding with the pre-breeding season of the little owl in Central Europe, from 1 March to 30 April (Johnson et al. 2009). This period coincides with the highest year-round vocal activity of little owls in Central Europe (Exo 1989, Finck 1990). The survey was carried out in good weather conditions (no or mild wind, no precipitation) as males are known to respond less actively in unsuitable weather (Hardouin et al. 2008). The minimum distance between two monitored

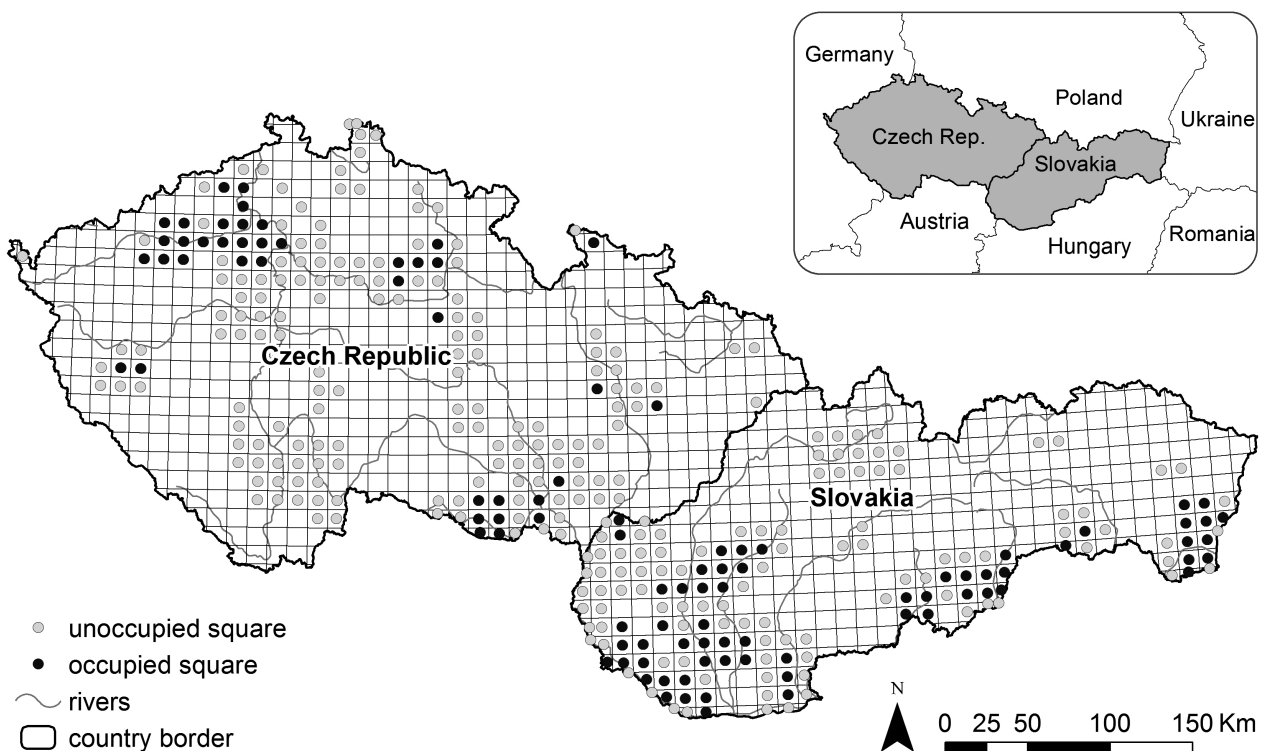
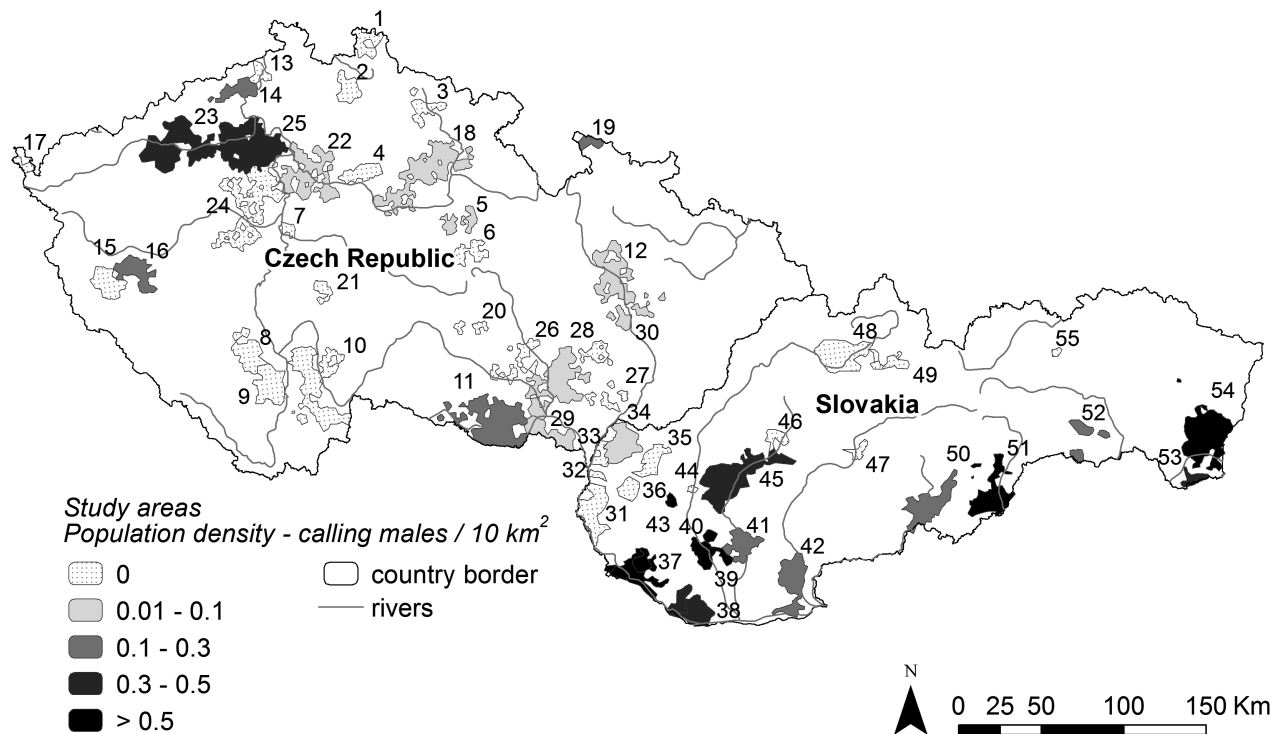


Fig. 1. Occupied and unoccupied mapping squares recorded during nationwide monitoring programmes of the little owl in the Czech Republic (2015-2016) and Slovakia (2009-2014).



**Fig. 2.** Distribution of individual study areas and area-specific population densities of the little owl recorded during nationwide monitoring programmes in the Czech Republic (2015-2016) and Slovakia (2009-2014).

localities was 500 m to prevent bias due to the high mobility of little owls (Zuberogoitia et al. 2011). Locations were considered occupied if an occurrence of the little owl was recorded at least once during the survey period. Population densities were measured as the number of calling males/10 km<sup>2</sup>. “Distribution centres” were defined as study areas with population densities exceeding 0.5 calling males/10 km<sup>2</sup> (Šálek & Schröpfer 2008, Šálek et al. 2013). Expected breeding places were determined as locations in little owl territories where repeated breeding behaviour or nests were recorded (Šálek & Schröpfer 2008, Šálek et al. 2013, Šálek 2014). Identification of the expected breeding places was locally supplemented with direct tracking for nests and communication with local stakeholders.

## Results

During the period 2009-2016, we monitored 2845 potential breeding localities. Of these, 1968 were located in the Czech Republic and 877 in Slovakia. In total, the presence of 325 calling males at 302 localities (94 males at 84 localities in the Czech Republic and 231 males at 218 localities in Slovakia) were recorded. The occurrence of the species was not confirmed at 2520 locations. In the Czech Republic, the little owl’s occurrence was recorded in 40 mapping squares, which represent 20.8 % of the mapping squares which were controlled for little owls (n = 192), however only 6.4 % of overall number of mapping squares on the country level (n = 628). In Slovakia, the little owl’s occurrence was confirmed in 61 mapping squares, which account for 37.7 % of

**Table 1.** Expected breeding places of the little owl recorded during nationwide monitoring programmes in the Czech Republic (2015-2016) and Slovakia (2009-2014).

	Czech Republic		Slovakia		Total	
	n	%	n	%	n	%
agricultural buildings	52	55.3	129	55.8	181	55.7
residential buildings	38	40.4	89	38.5	127	39.1
industrial buildings	2	2.1	8	3.5	10	3.1
churches & castles	2	2.1	3	1.3	5	1.5
orchards & gardens	0	0.0	2	0.9	2	0.6



controlled mapping squares ( $n = 162$ ) and 14.2 % of all available mapping squares ( $n = 429$ ) in the country (Fig. 1). The average population density of the little owl in all study areas across both countries was 0.19 calling males/10 km<sup>2</sup>. The average population density was, however, markedly higher in Slovakia (0.36 calling males/10 km<sup>2</sup>) than in the Czech Republic (0.09 calling males/10 km<sup>2</sup>). The population density in individual study areas also differed markedly (Fig. 2, Appendix 1). The highest recorded density was 1.19 (study area = 43) in Slovakia and 0.33 (study area = 23) calling males/10 km<sup>2</sup> in the Czech Republic (Fig. 2). The distribution centres were only located in Slovakia and comprised 11.3 % of the total area of the study areas in both the countries. In 55 % of the study areas (total area = 5946.7 km<sup>2</sup>) the occurrence of the little owl was not recorded in any year of the monitoring. The total breeding population size of the little owl was estimated at 130 breeding pairs in the Czech Republic and 550 pairs in Slovakia.

The analysis of expected breeding places of the little owl confirmed a strong preference for man-made objects over the original breeding sites in tree cavities (Table 1). From the total amount of 325 occupied territories, most expected breeding places were recorded in agricultural buildings (55.7 %), followed by residential buildings (39.1 %). Further expected breeding places were located in industrial buildings (2.1 %) and churches or castles (1.5 %). Two breeding places in natural habitats (orchards/gardens) were recorded and just one confirmed breeding place was recorded in a tree cavity, which was situated in an orchard within a human settlement.

## Discussion

Our study provides robust evidence about the current population status of the little owl in the Czech Republic and Slovakia, based on results of two nationwide monitoring programmes. These monitoring programmes provide the first coordinated large-scale programme of little owl monitoring in Slovakia and the most extensive research in the Czech Republic. As such, they may serve as important baselines for future analysis of changes in little owl distributions and population trends within both countries. In general, our research demonstrates steep population decline and range contraction of the little owl in both countries, which coincides with marked population decline of the species in other Central European regions (Ille 1996, Ille & Grinschgl 2001, Vogrin 2001, Źmihorski et al. 2006, van Nieuwenhuysse et al. 2008). The average population density, estimated across all study areas

in the Czech Republic and Slovakia, reached 0.19 calling males/10 km<sup>2</sup>. This is markedly lower than the population densities in neighbouring countries, e.g. in Poland (0.7 calling males/10 km<sup>2</sup>, van Nieuwenhuysse et al. 2008), Austria (0.3-2 calling males/10 km<sup>2</sup>, Ille & Grinschgl 2001) or Germany (1.4-1.7 calling males/10 km<sup>2</sup>, Zens 2005, van Nieuwenhuysse et al. 2008). However, there are marked differences in the little owl population densities recorded in the Czech Republic and Slovakia and across the individual study areas.

Due to previous nationwide monitoring programmes in the years 1993-2006 we could analyse changes in the little owl's large-scale population density in the Czech Republic. The current population density of 0.09 calling males/10 km<sup>2</sup> (2015-2016) is comparable with the density recorded in 2005-2006 (0.1 calling males/10 km<sup>2</sup>, Šálek & Schröpfer 2008) but declined about 73 % in comparison with the first monitoring programme in 1993-1995 (0.33 calling males/10 km<sup>2</sup>, Schröpfer 1996). In Slovakia, the lack of long-term data on population dynamics prevents detailed assessment of population density changes. However, the current population density (0.36 calling males/10 km<sup>2</sup>) is markedly lower than densities in 1995-1999 (0.75-1.1 calling males/10 km<sup>2</sup>, Pačenovský 2002) or local-scale studies performed during the 1980s and 1990s (e.g. 1.1-3.5 calling males/10 km<sup>2</sup>, Danko 1994, Danko et al. 1994). The population density in Slovakia, although in decline, is still markedly higher than the current average density in the Czech Republic.

Local-scale population densities of the little owl also differ, ranging from 0 to 1.2 calling males/10 km<sup>2</sup>. The majority of study areas have only low-medium population densities (Fig. 1, Appendix 1). These areas may be particularly sensitive to small decreases in the number of occupied localities, which may lead to further isolation and fragmentation of occupied localities resulting in rapid extinctions over large areas. Examples of rapid large-scale extinctions of the little owl have been documented in various regions of Southern Bohemia. In particular, Pykal et al. (1994) reported average population density of 0.24 calling males/10 km<sup>2</sup> in 1992 but that figure dropped to 0.09 calling males/10 km<sup>2</sup> in 2000 (Šálek & Berec 2001). During monitoring in the period 2005-2006, the species occurrence was not recorded (Šálek & Schröpfer 2008) and our own extensive monitoring during 2015-2016 likewise did not record occurrence of the species. In contrast to these instances of rapid extinctions and in line with previous studies in Central

and Western Europe (Šálek & Schröpfer 2008, van Nieuwenhuysse et al. 2008, Dobrý 2011, Šálek et al. 2013, Šálek 2014), we recorded several distribution centres (“high-density areas”) that represent current strongholds of the little owl distribution in studied regions. Although the number and area of these distribution centres cover only a small proportion of the total study areas, they may act as source populations of immigrants into the surrounding landscape (van Nieuwenhuysse et al. 2008, Šálek 2014). These areas were, however, situated only in Slovakia, especially in the southern and eastern lowland regions (Fig. 2, see also Dobrý 2011). In contrast to a previous monitoring programme during 2005 and 2006, which identified four areas in the Czech Republic (Šálek & Schröpfer 2008) this monitoring did not identify any distribution centres there. However, the identification of distribution centres may be affected by the spatial extent of individual study areas, as local high-density areas are more likely to be located in smaller study areas. For example, Šálek (2014) identified four local distribution centres where mean population density reached 1.52 calling males/10 km<sup>2</sup>. Those areas contained 86 % of all the calling males recorded in the study but accounted for only 15 % of the total area of the study region. Our study also indicates that large-scale extinctions and contractions of the distribution of the little owl have occurred during recent decades, although this pattern was more obvious in the Czech Republic. In particular, the occurrence of the little owl was not confirmed in 63 % of the study areas in the Czech Republic and 44 % in Slovakia (Fig. 2). In previous monitoring programmes in the Czech Republic, the percentage of unoccupied study areas increased from 0 % in 1993-1995 to 59 % in 1998-1999 and 66 % in 2005-2006 (Schröpfer 1996, 2000, Šálek & Schröpfer 2008). The percentage of unoccupied study areas in our monitoring across the Czech Republic (63 %) is comparable with the last monitoring programme in 2005-2006, although the total area of little owl monitoring increased by about 57 %. A contraction in the little owl’s range is also obvious when we compared the percentage of occupied quadrants recorded in our research (Fig. 1) with data from atlases of breeding bird distributions in the Czech Republic and Slovakia during the 1980s and 1990s (cf. Pačenovský 2002, Šťastný et al. 2006). This comparison demonstrates that the number of currently occupied quadrants dropped about 91 % in the Czech Republic and 74 % in Slovakia. The analysis of expected breeding places clearly shows that current breeding habitats of the little owl

are situated within man-made habitats in human settlements. Agricultural buildings, in particular farmsteads, are the most important breeding habitats of the little owl. This finding corresponds to previous research in the Czech Republic and Slovakia (Pačenovský 2002, Šálek & Schröpfer 2008, Dobrý 2011, Šálek 2014) and other Central European countries (van Nieuwenhuysse et al. 2008, Šálek et al. 2013). In particular, our previous study found that the occurrence of the little owl in the Central Europe was correlated with cover of farmsteads at nest- and home range- scale (Šálek et al. 2016). Farmsteads offer a high availability and diversity of suitable foraging, resting and breeding habitats for the little owl and several other farmland birds, including species of conservation concern (Hiron et al. 2013, Šálek et al. 2015a, Rosin et al. 2016, Šálek et al. unpublished data). The foraging and nesting suitability of farmsteads for the little owl and other farmland birds may substantially differ depending on the farmstead type. The majority of the little owl territories, but also higher abundance and diversity of other farmland birds, are placed within farmsteads with livestock breeding (Šálek et al. 2013, Šálek 2014, Šálek et al. unpublished data) or traditional farmsteads with old buildings that offer higher nest-site availability (Rosin et al. 2016). Breeding territories within residential buildings, which were identified as the second most preferred breeding place, are also predominantly situated in older residential areas within human settlements. The preference for older residential areas was also recorded for the little owl (van Nieuwenhuysse et al. 2008) and other cavity-breeding birds inhabiting urban environments (Šálek et al. 2015b). The original breeding habitats in the tree cavities within orchards or pollarded trees in farmland landscape accounted for the majority of little owl breeding places before the 1980s (Hudec 1983) but were confirmed in only one locality in 2010 – a nest located in an old orchard in southern Slovakia (Šipkovský 2012). The abandonment of natural breeding habitats was also recorded in other regions in the Central Europe (Haase 1993, Ille 1996, van Nieuwenhuysse et al. 2008). The main reasons for the long-term population decline of the little owl in Central Europe were dramatic changes and transformation of the agricultural landscape, which resulted in the loss of suitable foraging habitats (for further discussion see Loske 1986, Šálek & Schröpfer 2008, van Nieuwenhuysse et al. 2008). Habitat loss and fragmentation of grasslands (especially pastures and other grasslands with short-sward vegetation, which are crucial

foraging habitats of the little owl, see Grzywaczewski 2009, Šálek & Lövy 2012, Šálek et al. 2016), in connection with massive reduction of prey (e.g. large insect, small mammals), may result in food limitation during breeding season and thus lower breeding performance and higher adult mortality (Thorup et al. 2010). This factor was identified as an important driver of the little owl's decline in intensively used farmlands (Thorup et al. 2010, Šálek & Lövy 2012). However, we do not believe that the steep population decline of the little owl during recent decades was caused by this factor, as the area of grasslands, mostly represented by pastures, increased significantly during this period in the Czech Republic. This fact is also reflected in increases in the populations of many grassland-specialist birds (Reif & Hanzelka 2016). Little owl populations may also be severely influenced by harsh winters with lengthy snow cover and cold ambient temperatures, especially in regions where the continental climate has most influence (Exo & Hennes 1980, Exo 1988, van Nieuwenhuysse et al. 2008). For example, Schröpfer (2000) considered that rapid decline of the little owl between 1993 and 1999 in the Czech Republic was caused by harsh winters with long-standing snow cover. Climatic factors may also explain the ongoing retreat of the little owl distribution from previously occupied areas in the highlands (Pykal et al. 1994, Schröpfer 2000, Šálek & Schröpfer 2008). While our study recorded the highest population densities at the lowest altitudes, this topic needs more investigation. Destruction of original natural habitats in open farmland and a subsequent increase in the number of pairs breeding in human settlements (especially agricultural buildings), has also resulted in high anthropogenic mortality such as collisions with vehicles (Exo & Hennes 1980, Hernandez 1988, Génot 1995, Jacobsen 2006), mortality in anthropogenic traps (e.g. drowning in water reservoirs/basins, death in chimneys and hay blowers, Génot 1995, van Nieuwenhuysse et al. 2008) or high predation pressure from synanthropic mammalian predators (e.g. stone martens *Martes foina* and domestic cats *Felis domesticus*, Luder & Stange 2001, van Nieuwenhuysse et al. 2008). Road casualties and artificial traps have been identified as the main reasons for little owl non-natural mortality in the Czech Republic (Šálek et al. unpublished data) and thus mitigation of this threats may be important to stop population decline, especially in small and fragmented populations (Thorup et al. 2013).

Finally, increased population fragmentation, as a consequence of a declining habitat quality and low population densities, leads to isolation of individual sub-populations that are more prone to extinction due to deterministic and stochastic factors (Schaub et al. 2006, van Nieuwenhuysse et al. 2008).

In conclusion, our data demonstrate ongoing steep population decline and range contraction of the little owl in the Czech Republic and Slovakia, although the situation in the Czech Republic is more alarming. In the light of our results, the current population size of the little owl in the Czech Republic is estimated at 130 breeding pairs, which is an 87-94 % population decline compared to the period 1993-1995 (Schröpfer 1996). The estimated population size in Slovakia is markedly higher, totalling 550 breeding pairs. However, this estimate represents a 31-45 % reduction in the population compared to 1980-1999 (Pačénovský 2002). We propose that conservation authorities and conservation plans should respond immediately to this alarming situation with the introduction of short- and long-term measures to support remaining populations of the little owl. The little owl represents a sedentary species with small home ranges, high site fidelity of adults and short dispersal of offspring (van Nieuwenhuysse et al. 2008, Sunde et al. 2009, Šálek & Lövy 2012). As such, effective conservation measures for supporting high-quality foraging habitats (e.g. spatiotemporal grassland management in the little owl territories, Thorup et al. 2010, Jacobsen et al. 2016) and nesting opportunities (e.g. installation of predator-safe nest boxes, Bultot et al. 2001, van Nieuwenhuysse et al. 2008, Habel et al. 2015) or reducing of anthropogenic mortality (e.g. elimination of anthropogenic traps, Thorup et al. 2013, Šálek 2014) should be primarily implemented in recently occupied localities to facilitate dispersal and gene flow (stepping zones) between individual subpopulations.

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**Appendix 1.** Population density of the little owl in individual study areas in the Czech Republic and Slovakia.

Country	Study area	Area (km <sup>2</sup> )	Number of controlled localities	Number of calling males	Population density (calling males/10 km <sup>2</sup> )
Czech Republic	1	188.67	15	0	0
Czech Republic	2	181.65	14	0	0
Czech Republic	3	174.54	19	0	0
Czech Republic	4	192.09	76	0	0
Czech Republic	5	163.87	42	1	0.06
Czech Republic	6	168.00	24	0	0
Czech Republic	7	51.89	12	0	0
Czech Republic	8	298.64	40	0	0
Czech Republic	9	346.36	58	0	0
Czech Republic	10	778.09	145	0	0
Czech Republic	11	839.09	165	13	0.15
Czech Republic	12	689.58	115	2	0.03
Czech Republic	13	96.54	4	0	0
Czech Republic	14	200.77	31	4	0.2
Czech Republic	15	263.87	40	0	0
Czech Republic	16	295.58	74	7	0.24
Czech Republic	17	60.27	5	0	0
Czech Republic	18	812.65	168	6	0.07
Czech Republic	19	82.01	4	1	0.12
Czech Republic	20	72.09	8	0	0
Czech Republic	21	90.66	7	0	0
Czech Republic	22	597.41	127	1	0.02
Czech Republic	23	1672.04	314	56	0.33
Czech Republic	24	255.82	60	0	0
Czech Republic	25	555.43	135	0	0
Czech Republic	26	230.36	24	0	0
Czech Republic	27	125.77	16	0	0
Czech Republic	28	706.44	156	2	0.03
Czech Republic	29	254.78	37	1	0.04
Czech Republic	30	142.31	33	0	0
Slovakia	31	386.85	25	0	0
Slovakia	32	35.86	2	0	0
Slovakia	33	97.72	6	0	0
Slovakia	34	347.95	53	3	0.09

Slovakia	35	198.77	22	0	0
Slovakia	36	132.88	5	0	0
Slovakia	37	433.71	88	32	0.74
Slovakia	38	385.99	89	14	0.36
Slovakia	39	222.45	33	12	0.54
Slovakia	40	44.62	7	3	0.67
Slovakia	41	253.7	45	7	0.28
Slovakia	42	406.00	53	7	0.17
Slovakia	43	41.91	8	5	1.19
Slovakia	44	19.51	5	0	0
Slovakia	45	789.09	95	39	0.49
Slovakia	46	96.64	7	0	0
Slovakia	47	65.49	6	0	0
Slovakia	48	500.56	15	0	0
Slovakia	49	116.26	9	0	0
Slovakia	50	423.42	71	7	0.17
Slovakia	51	429.00	76	22	0.51
Slovakia	52	154.79	9	2	0.13
Slovakia	53	89.66	8	4	0.45
Slovakia	54	749.47	130	74	0.99
Slovakia	55	23.07	10	0	0

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