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ORIGINAL ARTICLE

Assessment of relative mortality rates for two rapidly declining farmland owls in the Czech Republic (Central Europe)

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Abstract

Anthropogenic mortality has a considerable impact on populations of long-lived species, such as raptors, which increasingly inhabit human-dominated landscapes. Here, we analyzed long-term mortality data for two rapidly declining owls, Little Owl *Athene noctua* and Barn Owl *Tyto alba,* in the Czech Republic. We evaluated relative mortality rates with respect to owl age, month of carcass recovery, and two time periods (before and after year 2000). We examined 961 mortality records (199 Little Owls and 762 Barn Owls) derived from six distinct database sources totally spanning the period of years 1934–2017 and the entire Czech Republic. Natural causes, entrapment in vertical hollow objects and drowning in liquid reservoirs (entrapment), and collision with vehicles accounted for the highest proportion of mortality cases in Little Owl, while collision with vehicles and entrapment represented the most important mortality sources in Barn Owl. Relative mortality rates in Little Owl caused by entrapment, non-vehicle collision, electrocution at power lines and confinement in buildings increased after the year 2000. In turn, the relative mortality rate due to collision with vehicles increased after 2000 in Barn Owl. Persecution, collision with vehicles, and entrapment accounted for higher relative mortality rates in first-year than adult Little Owls. In Barn Owls, higher relative mortality rates due to collision with vehicles and entrapment were detected in adult compared to first-year birds. Finally, relative mortality rates differed between age classes according to the month of carcass recovery for both species. For Little Owl, the highest relative mortality rates in first-year individuals were detected during July and September, whereas adult Little Owls suffered the highest relative mortality rates during March, November and December. In Barn Owls, the relative mortality rates of first-year individuals peaked in November and December, whereas adult birds suffered the highest relative mortality rate during July, January and February. This study strongly suggests that reducing the risk of anthropogenic mortality may be crucial to halt the decline of Little Owl and Barn Owl populations.

Keywords Urbanization · Anthropogenic mortality · Entrapment · Traffic · Seasonal changes · Population decline · Mitigation measures · Little Owl · Barn Owl

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Introduction

Anthropogenic disturbances and human population growth represent the key factors adversely affecting ecosystem functioning (Rands et al. 2010; Haddad et al. 2015), including the dynamics of communities and populations (e.g. August et al. 2002). Most avian populations are increasingly exposed to the risk of anthropogenic mortality due to various anthropogenic factors, such as collisions with buildings, windows, power lines, wind turbines or vehicles, electrocution at power lines or poisoning from pesticides (Longcore and Smith 2013; Loss et al. 2015). Anthropogenic mortality can have a considerable impact on local avian populations given the populations are small and fragmented (e.g. González et al. 2007). Moreover, anthropogenic mortality may cause drastic declines in the population also if it overlaps in time with natural mortality (Kokko 2001). While the impact of anthropogenic mortality on population declines has been considered in many songbirds (e.g. Mumme et al. 2000; Calvert et al. 2013), populations of large and long-lived species, such as owls and raptors, could be even more negatively influenced by anthropogenic mortality due to their longer generation times (Sergio et al. 2004; Martínez et al. 2006; González et al. 2007; Schaub et al. 2010; López-López et al. 2011).

Little Owl *Athene noctua* and Barn Owl *Tyto alba* are two avian predators whose distribution in Central Europe is currently restricted to urbanized landscapes (Poprach 2010; Šálek et al. 2013, 2016; Chrenková et al. 2017; Šálek 2014). Most European populations of both species declined sharply during the twentieth century, but in Central Europe, a large decline was documented only more recently (van Nieuwenhuyse et al. 2008; Barn Owl Trust 2012). In the Czech Republic, over the last two decades, the two species have undergone population declines of up to 94% (Little Owl) and 49% (Barn Owl), with the current population sizes estimated to be 130 and 150 breeding pairs for the Little Owl and Barn Owl, respectively (Šťastný et al. 2006; Chrenková et al. 2017; Poprach 2017). The rapid population declines and large-scale contractions of their distribution, including several local extinctions, have led to the inclusion of both species onto the national red list as critically endangered species (Šťastný et al. 2017) and the implementation of local and national conservation measures to support their populations (Diviš 2005; Poprach 2010, 2017).

Agricultural intensification resulting in massive degradation of suitable foraging and nesting habitats has been identified as a crucial factor behind Little Owl and Barn Owl population declines in many Western and Central European regions (e.g. de Bruijn 1994; van Nieuwenhuyse et al. 2008; Poprach 2010; Barn Owl Trust 2012; Šálek et al. 2016; Chrenková et al. 2017). Additionally, some studies indicate that direct anthropogenic mortality may increasingly contribute to the population declines in both owl species and accelerate their extinctions over large areas (van Nieuwenhuyse et al. 2008). For example, within the human-dominated landscape, the species may suffer increased mortality risks associated with collision with human-made objects or entrapment in buildings or water reservoirs. In fact, collision with vehicles has been suggested as the most important cause of anthropogenic mortality of Little Owl and Barn Owl (Hernandez 1988; Fajardo 2001; van Nieuwenhuyse et al. 2008). Yet, the thorough evaluation of the magnitude of natural and anthropogenic mortality sources is insufficient within and across avian species (Loss et al. 2015; but see Thorup et al. 2013 for Little Owl). In order to advance our understanding about the impacts of anthropogenic mortality on avian populations and to inform conservation management, it is required to 1) assess the magnitude of all mortality sources, 2) obtain mortality data throughout the annual cycle, and 3) address variation in mortality rates using large-scale data across extensive geographic areas (Loss et al. 2012, 2015).

The objective of this study was to comprehensively assess the relative rate of natural and anthropogenic mortality sources for two owl species of conservation concern, Little Owl and Barn Owl, in the Czech Republic. We examined mortality records by combining six different databases, totally spanning the period of years 1934–2017 and the entire Czech Republic. Firstly, in order to identify potential anthropogenic drivers of recent population declines in the two owls in the Czech Republic, we assessed differences in the relative rates of all mortality sources between the periods before and after year 2000. The negative impact of anthropogenic mortality on the dynamics of populations may vary depending on the age at death (e.g. Mumme et al. 2000) and on the time of season when mortality occurs (e.g. Kokko 2001). Therefore, secondly, for each owl species and for the entire study period we estimated mortality rates for adult and juvenile owls and for the month of year when an owl carcass was recovered.

Material and methods

The mortality data were obtained for the entire Czech Republic, Central Europe, which lies mostly between latitudes 48° and 51° N and longitudes 12° and 19° E. The country's climate is temperate continental with warm summers and cold winters and with most precipitation in spring and autumn months.

The Little Owl is a sedentary species with stable home ranges covering up to 50 ha and with low offspring dispersal distances (mostly up to 20 km from the natal place; Cepák et al. 2008, van Nieuwenhuyse et al. 2008). The Barn Owl is a non-territorial species with home ranges extending up to 5000 ha (Barn Owl Trust 2012). In the Czech Republic, offspring Barn Owls disperse on average 63 km from their natal sites (Cepák et al. 2008).

We analyzed data from the following database sources: (i) Bird Ringing Centre (National Museum Prague) encompassing recoveries of dead owls during 1934–2016 ($n = 381$), (ii) Wildlife Rehabilitation Centres (Czech Union for Nature Conservation) covering the period 2006–2016 ($n = 124$), (iii) "Free wings database of the Czech Society for Ornithology" gathering data about illegal persecution of birds covering the period 2000–2017 ($n = 3$), (iv) "Faunistic database of the Czech Society For Ornithology" (http://birds.cz/avif) covering the period 1972–2017 ($n = 16$), (v) radio-tracking data gathered in 2000 and 2017 ($n = 6$; Šálek et al. 2010; Šálek and Lövy 2012; J. Vlček, in litt.), (vi) database of members of "Working group on protection and research of birds of prey and owls of the Czech Society for Ornithology" covering the period 1954–2017 ($n = 177$), and (vii) personal databases of owl specialists (authors) who gathered long-term data (1950–2017) about the mortality of both owl species across the Czech Republic ($n = 257$). The latter source consists mostly of records gathered from interviews with farmers and local stakeholders or by directly searching for carcasses in areas with the occurrence of both species.

We identified six sources of mortality: 1) natural mortality, including starvation and predation (by wild and domestic animals), 2) anthropogenic mortality from collision with vehicles (automobiles and trains), 3) anthropogenic mortality from entrapment in the form of inescapable physical restraint leading to rapid death by suffocation, choking, hypothermia or physical trauma (e.g. fractures, burn injuries), including entrapment in tight hollow human structures (e.g. vertically standing pipes, ventilation tubes, hay blowers, chimneys) and drowning in liquid reservoirs (e.g. steep-sided reservoirs and tanks for water and molasses, water barrels, livestock drinkers; see also Fig. 1), 4) anthropogenic mortality from direct persecution, including shooting and poisoning, 5) other less frequently reported sources of anthropogenic mortality, including cases when birds were accidentally trapped in buildings and died of starvation, non-vehicle collision (e.g. collisions with windows, glass walls, power lines), and electrocution at power lines, and 6) unknown causes. The age of dead birds was categorized as 1 CY (i.e. birds in their first calendar year) or adult (i.e. birds in their second calendar year or older; see also Molina-López et al. 2011). To assess long-term temporal differences in owl relative mortality rates, the difference was examined for two time periods: before and after the year 2000 (i.e. 1934–1999 vs. 2000–2017).

Statistical analysis

Differences in relative mortality rates were examined for both owl species with generalized linear mixed models (GLMM), assuming binomial distribution of errors. The relative mortality rate was examined as a proportion of dead birds per mortality subgroup (Appendix S1). Because mortality records did not always include information about the age at death and about the month when death occurred, different datasets and GLMMs were used to test differences in relative mortality rates according to 1) time period, mortality source and owl species; 2) age class and mortality source; and 3) age class and month (Appendix S1). Different database sources were selected for the above tests to address the problem that mortality data were gathered over different years and with uneven intensities (see above). Namely, databases i), vi), and vii) were selected for GLMM on temporal period and mortality source (GLMM 1), whereas databases i), ii), vi), and vii) were selected for GLMMs on age class, mortality source and month (GLMMs 2 and 3). The total number of dead birds per all mortality subgroups (the binomial denominator, Appendix S1) was used as a prior weight in all GLMMs to address variation in samples sizes. The source of databases was used as a random factor in all GLMMs. Also, since relative mortality rates varied markedly among mortality sources within individual databases, intercepts were allowed to vary randomly among databases within mortality sources (random intercept GLMMs 2 and 3) and among databases within mortality sources and owl species (random intercept GLMM 1, see Appendix S1). All tests were performed and parameter estimates of fixed effects were calculated with *lme4* package (Bates et al. 2015) in R software (R Core Team 2018). Type-3 Wald chi-square tests evaluating the significance of fixed effects of corresponding GLMMs were calculated with *car* package (Fox and Weisberg 2011).

Results

We compiled data on 961 mortality records, involving 199 Little Owl and 762 Barn Owl mortality events (Table 1) from the whole area of the Czech Republic during the period 1934–2017 (Appendix S2). Entrapment in hollow objects and drowning in liquid reservoirs (hereafter entrapment) accounted – in absolute terms – for the highest proportion of mortality records in Little Owl (23.6%, Table 1). This mortality source was closely followed by mortality from collision with vehicles (20.6%) and by natural mortality (14.6%, Table 1). Collision with vehicles was by far the most reported mortality source in Barn Owl (41.5%); entrapment being the second most frequent one (26.1%, Table 1).

After combining data from three representative databases, GLMM revealed that relative mortality rates have different trends between two time periods for six mortality sources in Little Owl and Barn Owl (GLMM 1, Type-3 test for the highest interaction term: owl species × time period × mortality source, $\chi2 = 192.3$, $df = 5$, $P < 0.0001$; Appendix 3). Out of the known mortality sources, entrapment, collision with vehicles, and natural mortality accounted for the highest proportion of mortality records in Little Owl, while collision with

Fig. 1 Examples of Little Owl and Barn Owl anthropogenic mortality in terms of entrapment: **a** drowned juvenile Little Owl in a water reservoir (livestock drinker), Photo: Ronald van Harxen, **b** 59 drowned birds found in a single reservoir (molasses tank), including ten Barn Owls and one Little Owl, Photo: Karel Poprach, **c** two adult Little Owls caught in a hollow object (vertically standing pipe), Photo: Ronald van Harxen, **d** five dead Barn Owls caught in a hollow object (hay blower), Photo: Karel Poprach

vehicles and entrapment represented the most important mortality sources in Barn Owl (Fig. 2). Importantly, while the relative mortality rates due to entrapment and due to non-vehicle collision, electrocution at power lines and confinement in buildings (i.e. other anthropogenic mortality) increased after year 2000 in Little Owl, the trend for these mortality sources was the opposite in Barn Owl (Fig. 2). In contrast, while the relative mortality rate due to collision with

Table 1 Number and percentage (%) of mortality cases per mortality source for first-year (1CY), adult (AD) and all individuals (total) of Little Owl *Athene noctua* and Barn Owl *Tyto alba* in the Czech Republic during 1934–2017. The values for "total" refer to all mortality cases including owls of unknown age. Mortality sources marked in italics were examined in statistical analyses as distinct categories

	Little Owl *Athene noctua*						Barn Owl *Tyto alba*					
	1CY	%	AD	%	Total	%	1CY	%	AD	%	Total	%
Natural mortality												
Starvation	6	8.6	3	5.5	10	5.0	3	1.8	18	4.3	30	3.9
Predation	11	15.7	8	14.5	19	9.5	5	2.9	9	2.2	19	2.5
Anthropogenic mortality												
Collision with vehicles												
Collision with automobiles	16	22.9	12	21.8	37	18.6	75	43.9	157	37.9	289	37.9
Collision with trains	2	2.9	2	3.6	4	2.0	3	1.8	18	4.3	27	3.5
Entrapment												
Entrapment in hollow objects	8	11.4	5	9.1	19	9.5	17	9.9	77	18.6	136	17.8
Drowning in liquid reservoirs	14	20.0	8	14.5	28	14.1	11	6.4	46	11.1	63	8.3
Persecution												
Shooting	1	1.4	6	10.9	14	7.0	1	0.6	5	1.2	12	1.6
Poisoning	4	5.7	0	0.0	4	2.0	5	2.9	2	0.5	8	1.0
Other sources												
Collision with power lines and buildings	1	1.4	2	3.6	3	1.5	8	4.7	6	1.4	20	2.6
Electrocution at power lines	1	1.4	2	3.6	4	2.0	4	2.3	10	2.4	24	3.1
Starvation after confinement in buildings	0	0.0	0	0.0	0	0.0	14	8.2	13	3.1	27	3.5
Unknown sources	6	8.6	7	12.7	57	28.6	25	14.6	53	12.8	107	14.0

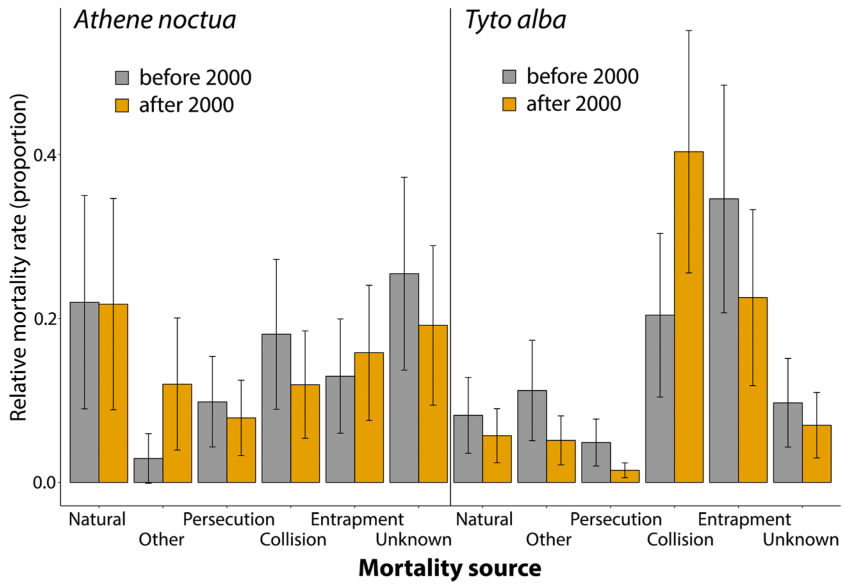

Fig. 2 Relative mortality rates in Little Owl *Athene noctua* and Barn Owl *Tyto alba* before and after year 2000 in the Czech Republic. Estimated relative mortality rates are back-transformed to proportions after a binomial GLMM; error bars are + 1SE. Relative mortality rate was examined for the period of years 1934–2017. The meaning of anthropogenic mortality sources is as follows: *Entrapment*—entrapment in hollow objects and liquid reservoirs, *Collision*—collision with vehicles, *Persecution*—shooting and poisoning, *Other*—non-vehicle collision, electrocution at power lines, and confinement in buildings

vehicles decreased after 2000 in Little Owl, the relative mortality rate for this source sharply increased after 2000 in Barn Owl (Fig. 2).

A comparison of mortality sources between first-year and adult individuals revealed significant differences in relative mortality rates for both owl species (GLMM 2A-B, Type-3 tests for the highest interaction terms: age class × mortality source, Little Owl, $\chi2 = 161.97$, $df = 5$, $P < 0.0001$; Barn Owl, $\chi2 = 3331.59$, $df = 5$, $P < 0.0001$; Figs. 3 and 4; Appendix S3). In particular, persecution accounted for higher relative mortality rates in first-year than adult Little Owls, but the opposite was revealed for non-vehicle collision, electrocution at power lines and confinement in buildings in this species (Fig. 3). Relative mortality rates due to collision with vehicles and entrapment were higher for first-year than adult Little Owls (Fig. 3). As for the Barn Owl, the largest relative mortality rate differences between age classes were revealed for collision with vehicles and entrapment, with carcasses of adults being recovered more frequently than those of first-year owls (Fig. 4).

Finally, relative mortality rates also differed between age classes according to the month of year for both species (GLMM 3A-B, Type-3 tests for the highest interaction terms: age class × month of year, Little Owl, $\chi2 = 87.72$, $df = 4$, $P < 0.001$; Barn Owl, $\chi2 = 4867.08$, $df = 6$, $P < 0.001$; Figs. 5 and 6; Appendix S3). For Little Owl, the highest relative mortality rates in first-year individuals were detected during July and September, whereas adult Little Owls suffered the highest relative mortality during March, November and December (Fig. 5). In Barn Owl, relative mortality rates in first-year

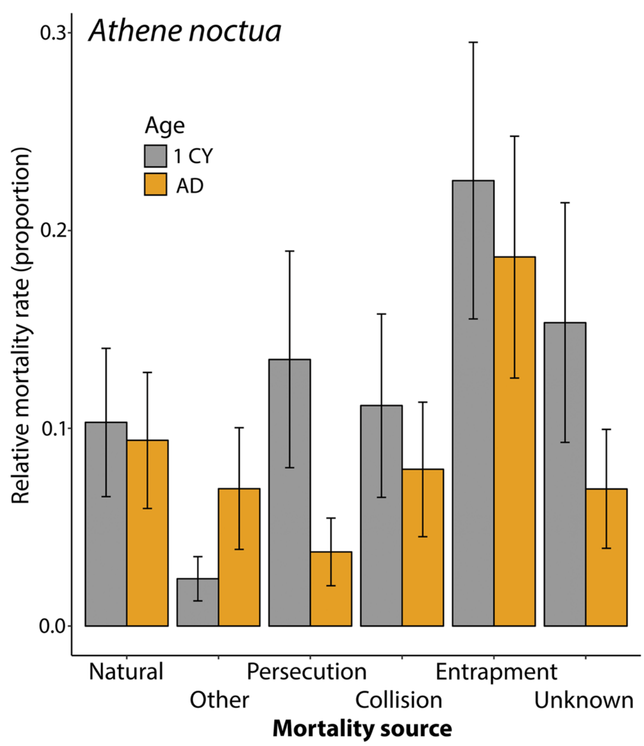

Fig. 3 Relative mortality rates for six mortality sources between first-year (1 CY) and adult (AD) Little Owls *A. noctua* in the Czech Republic. Estimated relative mortality rates are back-transformed to proportions after a binomial GLMM; error bars are + 1SE. Relative mortality rate was examined for the period of years 1934–2017. The meaning of anthropogenic mortality sources is as follows: *Entrapment*—entrapment in hollow objects and liquid reservoirs, *Collision*—collision with vehicles, *Persecution*—shooting and poisoning, *Other*—non-vehicle collision, electrocution at power lines and confinement in buildings

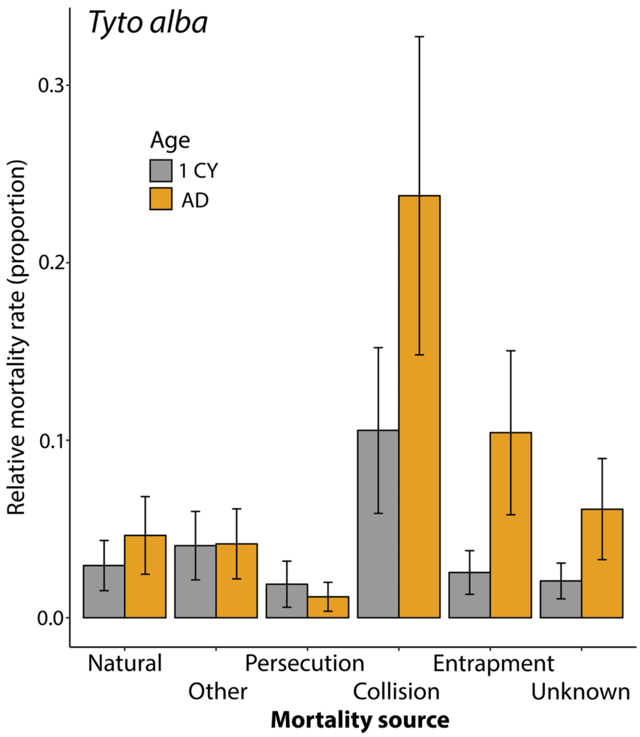

Fig. 4 Relative mortality rates for six mortality sources between first-year (1 CY) and adult (AD) Barn Owls *T. alba* in the Czech Republic. Estimated relative mortality rates are back-transformed to proportions after a binomial GLMM; error bars are + 1SE. Relative mortality rate was examined for the period of years 1934–2017. The meaning of anthropogenic mortality sources is as follows: *Entrapment*—entrapment in hollow objects and liquid reservoirs, *Collision*—collision with vehicles, *Persecution*—shooting and poisoning, *Other*—non-vehicle collision, electrocution at power lines and confinement in buildings

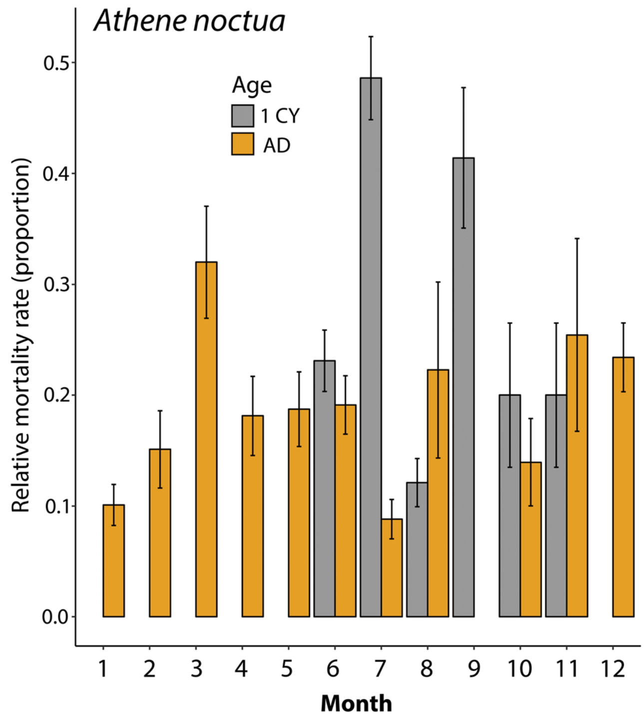

Fig. 5 Relative mortality rates during individual months between first-year (1 CY) and adult (AD) Little Owls *A. noctua* in the Czech Republic. Estimated relative mortality rates are back-transformed to proportions after a binomial GLMM; error bars are +1SE. Relative mortality rate was examined for the period of years 1934–2017

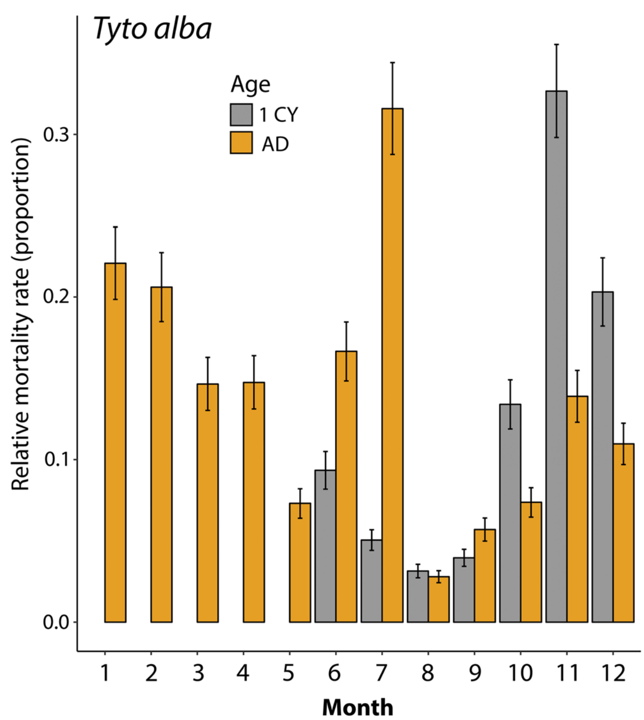

Fig. 6 Relative mortality rates during individual months between first-year (1 CY) and adult (AD) Barn Owls *T. alba* in the Czech Republic. Estimated relative mortality rates are back-transformed to proportions after a binomial GLMM; error bars are + 1SE. Relative mortality rate was examined for the period of years 1934–2017

individuals were highest in November and December, whereas adult Barn Owls suffered the highest relative mortality during July, January and February (Fig. 6).

Discussion

This study offers the first comprehensive evaluation of Little Owl and Barn Owl mortality in the Czech Republic, a country where rapid and large-scale contractions of the two owls' ranges have recently been recorded. Consistent with previous studies (Tables 1 and 2), our results show that anthropogenic sources account for a high percentage of direct mortality in the two species. Naef-Daenzer et al. (2017) suggested that conclusions about the impact of anthropogenic mortality on species populations may be considerably overestimated if based on data from only one source (e.g. ringing recoveries). On the other hand, the magnitude of natural mortality may be underrepresented in mortality records as the recovery probability of predated individuals is low and mortality due to starvation is difficult to assess (Naef-Daenzer et al. 2017). Importantly, our datasets were derived from an array of distinct sources and

Table 2 Number and percentage (%) of Little Owl *A. noctua* and Barn Owl *T. alba* mortality in the Czech Republic before and after year 2000. The values refer to all mortality cases including owls of unknown age. Mortality sources marked in italics were examined in statistical analyses as distinct categories

	Little Owl *Athene noctua*				Barn Owl *Tyto alba*			
	Before 2000		After 2000		Before 2000		After 2000	
	n	%	*n*	%	*n*	%	*n*	%
Natural mortality								
Starvation	2	1.8	8	8.9	3	1.6	27	4.7
Predation	8	7.3	11	12.2	4	2.1	15	2.6
Anthropogenic mortality								
Collision with vehicles								
Collision with automobiles	16	14.7	21	23.3	33	17.4	256	44.8
Collision with trains	3	2.8	1	1.1	9	4.7	18	3.1
Entrapment								
Entrapment in hollow objects	3	2.8	16	17.8	43	22.6	93	16.3
Drowning in liquid reservoirs	10	9.2	18	20.0	37	19.5	26	4.5
Persecution								
Shooting	13	11.9	1	1.1	9	4.7	3	0.5
Poisoning	0	0.0	4	4.4	1	0.5	7	1.2
Other sources								
Collision with power lines and buildings	0	0.0	3	3.3	11	5.8	9	1.6
Electrocution at power lines	2	1.8	2	2.2	2	1.1	22	3.8
Starvation after confinement in buildings	0	0.0	0	0.0	8	4.2	19	3.3
Unknown sources	52	47.7	5	5.6	30	15.8	77	13.5

thus allow robust evaluation of mortality sources and their relative importance.

In accordance with previous studies (Tables 1 and 2), we found that collision with vehicles represents an important cause of mortalities in both Barn Owl and Little Owl, though collision with vehicles contributed more highly to the overall mortality in Barn Owl compared to Little Owl (Fig. 2). The high mortality rate due to collision with vehicles in Barn Owl is usually interpreted as a consequence of large (daily and year-round) home ranges and dispersal activity, which makes Barn Owl, compared e.g. to Little Owl, more prone to traffic accidents (van Nieuwenhuyse et al. 2008; Barn Owl Trust 2012). The higher relative mortality due to collision with vehicles, predominantly automobiles, can also reflect an increased use of road verges as an alternative foraging habitat by Barn Owls (de Jong et al. 2018). Previous evidence has indicated that road margins are attractive foraging habitats for Barn Owls especially during autumn and winter months when the abundance of small mammals (i.e. main prey of Barn Owl) is reduced, making the road verges an attractive sink (high-collision risk) habitat (Massemin et al. 1998; Grilo et al. 2012, 2014; de Jong et al. 2018). The elevated relative mortality from collision with vehicles in Barn Owl after year 2000 likely reflects increased road density and traffic volumes in the Czech Republic during the last decades (Cikánková et al. 2014), thereby corresponding to previous research results from Western Europe (de Bruijn 1994; Newton et al. 1997).

Our analyses also reveal considerably high relative mortality rates linked to entrapment in hollow objects and drowning in liquid reservoirs (entrapment). The relative rates of this mortality source revealed by our analyses exceed most of the previously published rates for the two owl species across Europe. In our study, entrapment absolutely accounted for 23.6 and 26.1% of the total mortality of Little Owl and Barn Owl, respectively. In other European countries, this mortality source accounted for 4.5–17% of the total mortality of Little Owl and for 0–9.8% of Barn Owl total mortality (Tables 3 and 4). Moreover, it is likely that the actual mortality rates related to entrapment could even be underestimated (see also de Bruijn 1994; Poprach 2010; Barn Owl Trust 2012), as bird carcasses may be inconspicuous or inaccessible in hollow objects or liquid reservoirs. In fact, the comparison of ring recovery data with data collected in the field by owl specialists (i.e., records from interviews with farmers and local stakeholders or by directly searching for carcasses in areas of occurrence of both species), reveals that the absolute mortality rate due to entrapment was 7% using the ring recovery method, while it represented 72% of the cases detected during fieldwork by owl specialists. Only a few studies have evaluated the importance of entrapment for the mortality of owls and other bird species. For example, a study in which 2513 farmsteads in the Czech Republic were controlled for farm water reservoirs found that 10% of the investigated farmsteads included such reservoirs (Machar and Poprach 2012). From a

Table 3 Review of Little Owl *A. noctua* mortality rates reported from various European countries[a]

	South Germany 1955–2012 ring recoveries $n = 465$	South Germany 2009–2012 radio-telemetry $n = 177$	Germany 1966–1974 ring recoveries $n = 251$	Great Britain 1910–1969 ring recoveries $n = 199$	Belgium 1989–1993 ring recoveries	Belgium 1991–2001 bird care centers $n = 1261$	Netherlands 1917–1994 ring recoveries $n = 152$
Natural mortality							
Starvation	1.7		5.2	2	–	–	4.6
Predation	4.7	76.2	0.8	2	20.2	1.7	10.5
Anthropogenic mortality							
Collision with vehicles		6.2			34	31.2	
Collision with automobiles	22.8		16.7	12.1	–	–	9.9
Collision with trains	1.9		3.6	9.5	–	–	0
Entrapment		3.4 [c]					
Entrapment in hollow objects	6		6	2.5	7.4	12.3	0
Drowning in liquid reservoirs	6.7		4	2	9.6	0	7.2
Persecution							
Shooting	0.4		1.2	22.1	–	–	0
Poisoning	–		–	–	3.2	3	0
Other sources							
Collision with power lines and buildings	3.2		2.4	1.5	–	–	0.7
Electrocution at power lines	0.2		0	1.5	–	–	0.7
Starvation after confinement in buildings	0.4		–	–	–	–	2.6
Various [b]	10.5	6.2	0	5	0	22.6	2.6
Unknown sources	41.3	7.9	60.2	39.7	25.5	29.2	61.2

[a] Sources: Glue (1971); Exo and Hennes (1980); Bultot et al. (2001); Le Gouar et al. (2011); Naef-Daenzer et al. (2017)

[b] In the original papers this category mostly referred to unspecified trauma, birds found in nest box, orphaned young or disease

[c] In the original paper, this category referred to mortality associated with "human structures"

Table 4 Review of Barn Owl *T. alba* mortality rates reported from various European countries[a]

	Great Britain 1963–1996 multiple sources n = 1067	Spain 1990–1999 multiple sources n = 173	Spain 1983–1989 multiple sources n = 347	Netherlands 1967–1975 multiple sources n = 41	Netherlands 1976–1984 multiple sources n = 49
Natural mortality					
Starvation	25.8	–	4.3	14.6	18.4
Predation	1.7	–	–	0	2
Disease	3.3			0	0
Anthropogenic mortality					
Collision with vehicles					
Collision with automobiles	44.7	80.9	36.5	26.8	53.1
Collision with trains	–	–	–	4.9	4.1
Entrapment					
Entrapment in hollow objects	–	–	–	0	0
Drowning in liquid reservoirs	1.1	–	–	9.8	4.1
Persecution					
Shooting	1	1.7	15.5	12.2	2
Poisoning	6.1	2.3	2	9.8	0
Other sources					
Collision with power lines and buildings	–	1.2	2.5	9.8	8.2
Electrocution at power lines	0.4	2.9	2.5	0	0
Starvation after confinement in buildings	–	1.2	4	12.2	8.2
Various [b]	7.5	9.8	32.9		–
Unknown sources	8.4				–

[a] Sources: de Bruijn (1994); Newton et al. (1997); Fajardo (2001)

[b] In the original papers this category mostly referred to unspecified trauma, birds found in nest box, orphaned young or disease

total of 396 water reservoirs, drowned birds (965 individuals) were found in 20% of them, with Barn Owl carcasses (44 individuals) recorded in 5% of the reservoirs and Little Owl carcasses (6 individuals) recorded in 1.5% of the reservoirs. The total number of drowned birds might have been even higher, as the authors were mostly able to record only the carcasses on the water surface. Drowning in various liquid reservoirs was considered as a significant cause of raptor mortality for some species (Craig and Powers 1976; Ellis et al. 2010), including species of conservation concern (Anderson et al. 1999). Substantial mortality in various artificial vertical hollow objects (e.g. chimneys, tubular poles, hay blowers) was documented for Little Owl and Barn Owl, but also for other cavity-nesting birds, in various countries (Clech 1993; van Nieuwenhuyse et al. 2008; Barn Owl Trust 2012; Malo et al. 2016). Intriguingly, we found that while mortality rates linked to entrapment, non-vehicle collision, electrocution at power lines and confinement in buildings increased in Little Owl in the last two decades, the trend was opposite in Barn Owl. We suggest that these changes reflect the shifts in breeding distribution from farmland to urbanized landscapes, which have recently been more pronounced for Little Owl than Barn Owl (Šálek and Schröpfer 2008; Chrenková et al. 2017). Also, it is possible that the decrease in Barn Owl mortality rates with respect to entrapment in hollow objects is the consequence of intensive nest-box management programs, with most Barn Owls currently nesting in specially designed nest boxes in the Czech Republic (Poprach 2017). The latter idea on the effect of nest-site suitability or safety is corroborated by our results on adult mortality in Little Owl, which was seasonally highest during March, i.e., around the egg-laying period when adult birds select or start to reproduce at nest sites. Importantly, while the relative mortality rate due to entrapment was lower in Barn Owl compared to Little Owl, the seasonally highest mortality rate of adult Barn Owls during July (Fig. 6) was relatively more frequently attributed, both before and after 2000, to entrapment than any other natural or anthropogenic source of mortality. Therefore, our study suggests that entrapment can contribute importantly to population declines in both owls in the Czech Republic.

Finally, a surprisingly high relative mortality rate of first-year Little Owls due to poisoning (Fig. 3) suggests that stricter control of agrochemical application and storage would be an important feature of Little Owl conservation plans (Hindmarch et al. 2017). The latter mortality factor may not be trivial, because many cases of mortality are classified as natural (e.g. apparent starvation) or unknown (unclear causes of death), which comprise most of the mortality cases in the Little Owl (Figs. 2 and 3), may be at least partly associated with poisoning. Therefore, future studies should invest in identifying the causes of mortality in Little Owl when the reason of death is unknown or questionable (e.g. starvation).

Conservation implications

Agricultural intensification and subsequent loss of suitable foraging and nesting habitats (bottom-up effect) and predation (top-down effect) have previously been identified as crucial factors in Little Owl and Barn Owl population declines (e.g. van Nieuwenhuyse et al. 2008; Barn Owl Trust 2012; Naef-Daenzer et al. 2017). Our study strongly indicates that direct anthropogenic mortality, especially collision with vehicles and entrapment, may significantly contribute to these declines in the Czech Republic. In order to improve the population status of these owl species, in addition to foraging habitat restoration, the focus should be on the reduction of risks of collision with vehicles and various forms of entrapment in urbanized landscapes (Ellis et al. 2010; Malo et al. 2016). The consequences of Barn Owl nest-site supplementation in the Czech Republic suggest that the provisioning of safe sites for nesting and roosting also for the Little Owl could be an effective measure to decrease mortality from entrapment in hollow objects, as well as from some sources of natural mortality (e.g. predation on adults and/or nestlings at the nest). To reduce the mortality risk caused by collision with vehicles, mainly automobiles, conservation measures should enhance habitat heterogeneity of agricultural landscapes, especially rodent-rich habitats including set-aside patches, field margins and other non-cropped elements (Tattersall et al. 1999; Dicks et al. 2014; de Jong et al. 2018). Moreover, grassland strips parallel to road verges should be established at least in road mortality hotspots to keep foraging owls further from roads (Grilo et al. 2012). Nevertheless, it seems inevitable that the management of roadside verges should also be changed in the short term, e.g. by maintaining shrubs instead of grass along roads (see Boves and Belthoff 2012; Arnold et al. 2018).

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