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Vocal activity of the Central European Boreal Owl population in relation to varying environmental conditions

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Vocal activity is one of the main attributes that enables assessment of the presence and abundance of animal populations. However, the factors affecting vocal activity are rarely studied, especially in owls. We studied the vocal activity of Boreal Owl (*Aegolius funereus*) using acoustic monitoring in relation to environmental factors in Central Europe (Czech Republic), over an area of 100 km^2. We analysed a total of 1,310 hours of sound recordings collected over two years (2015 and 2016) at the turn of March/April and April/May. The frequency of sampling points in which we recorded Boreal Owl vocalizations varied from 0.17 to 0.59 and was higher in the year of increased prey abundance (2015) and earlier in the breeding season (March/April). The duration of Boreal Owl vocal activity varied from 1 to 60 minutes per hour and was related to temporal factors. In particular, the duration of Boreal Owl vocalization increased late in the breeding season (April/May) and in the year of higher prey abundance (2015), and it showed two peaks of vocal activity during the night. Weather conditions, the occurrence of nesting Boreal Owl pairs, and the vocalization of other owl species had no effect on the duration of Boreal Owl vocalization. These findings highlight the importance of between-year, seasonal, and within-night variability in the Boreal Owl vocal activity and document that acoustic monitoring based on sound recorders works well for monitoring of nocturnal bird species.

1. Introduction

Vocal communication represents an effective way for animals to transmit information between each other. They use a wide range of sounds for defending territory, attracting mates, deterring predators, navigating, finding food, and staying in touch with members of their social group (Marler & Slabbekoorn 2004, Catchpole & Slater 2008, Bradbury & Vehrencamp 2011). Acoustic monitoring using modern technologies, including sound recordings (Blumstein *et al.* 2011), enables us to detect vocal activities over a wide range of wavelengths, from ultrasound to infrasound (Whytock & Christie 2017), for long time intervals (Frommolt 2017, Whytock & Christie 2017), and under different temporal (Tremain *et al.* 2008, Odom & Mennill 2010) and spatial conditions (Blumstein *et al.* 2011, Hodge *et al.* 2013, Deichmann *et al.* 2017). Using acoustic methods we can also reveal the presence/absence of a species and their abundance (Fischer *et al.* 1997,

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Haselmayer & Quinn 2000, MacSwiney *et al.* 2008), identify individuals, their age and gender (Blumstein *et al.* 2011), and variations in vocal spectrum and singing style (Forstmeier & Balsby 2002, Brunner & Pasinelli 2010, Halfwerk *et al.* 2011). However, despite the availability of various information, studies describing vocal patterns in birds, particularly in owls, are still needed (Kloubec 2007, Kloubec & Čapek 2012, Rasmussen *et al.* 2012).

Nocturnal bird species use vocalizations to defend their territories, attract mates, or to maintain communication within pairs (e.g., Ganey 1990, Penteriani 2002, Odom & Mennill 2010). The vocal activity of nocturnal birds can vary with biotic and abiotic factors. One of such factors is the time of year with the calling peak occurring during reproduction (Slagsvold 1977, Clark & Anderson 1997, Amrhein *et al.* 2002, Kloubec & Čapek 2012), and another factor is the time of day with the highest calling frequency around dusk and dawn (Kloubec & Pačenovský 1996, Clark & Anderson 1997, Mougeot & Bretagnolle 2000, Kloubec 2007).

'The vocal activity of nocturnal birds can be also related to prey abundance (Lundberg 1980, Swengel & Swengel 1995), weather conditions (Slagsvold 1977, Lengagne & Slater 2002), the occurrence of second or replacement clutches and the presence of unpaired mates (Galeotti & Pavan 1993, Amrhein *et al.* 2002, Kloubec 2007), or inter-specific competition (Crozier *et al.* 2006, Zuberogoitia *et al.* 2008, Lourenco *et al.* 2013). However, comprehensive analyses of factors affecting vocal activity, including food and weather conditions, circadian and circannual patterns, and intra- and inter-specific competition are especially rare in owls (Kloubec & Čapek 2012, La 2012).

The Boreal Owl (*Aegolius funereus*) is a small, nocturnal, "sit and wait" avian predator with a Holarctic breeding range. It feeds on voles in Northern Europe (Korpimäki & Hakkarainen 2012) and voles and mice in Central Europe (Zárybnická *et al.* 2011, 2013). This owl inhabits predominantly old-growth coniferous forests (Šťastný *et al.* 2006, Korpimäki & Hakkarainen 2012, Zárybnická *et al.* 2017) and places its nests in natural tree cavities and nest boxes (Korpimäki & Hakkarainen 2012, Zárybnická *et al.* 2015a). Timing of breeding, clutch size, reproductive success, home range size, and parental care are influenced by food abundance (*Apodemus* mice and *Microtus* voles in Central Europe) and changes greatly between years and during the breeding season (Zárybnická *et al.* 2013, Zárybnická & Vojar 2013, Zárybnická *et al.* 2015a, b, Kouba *et al.* 2017). Boreal Owls usually breed between March and July (Korpimäki & Hakkarainen 2012, Zárybnická *et al.* 2012) using their calls to defend their territories and to attract mates (Mikkola 1983).

Vocalizations of Czech Boreal Owls are performed from February to May, peaking in early season during March and April (Vacík 1991, Kloubec 2007). Their vocalizations are usually detectable up to a distance of 0.5–1 km, or 1–3 km during more suitable weather conditions (Vacík 1991, Kloubec & Pačenovský 1996). Vocal activity usually varies according to food supply (Palmer 1987, Kloubec & Pačenovský 1996), during the course of the night (Kloubec & Pačenovský 1996), and it can be reduced during inclement weather (Mikkola 1983, Palmer 1987, Kloubec & Pačenovský 1996, Kloubec 2007). It may also be affected by con- and heterospecifics. In particular, vocal activity may be increased with increasing density of Boreal Owl individuals (Kloubec 1986, König *et al.* 1999).

Boreal Owls avoid territories of their competitors and predators, for example Tawny Owl (*Strix aluco*) (Vrezec & Tome 2004) or Ural Owl (*Strix uralensis*) (Hakkarainen & Korpimäki 1996), suggesting that vocalizations of Boreal Owls may also be influenced by the presence of other owl species. However, individual studies have usually focused separately on particular effects, without a comprehensive approach allowing us to understand the relative significance of individual factors to Boreal Owl vocalization. Moreover, most studies have been performed based on a standard method of vocal registration by individual observers during selected parts of the night and they often used voice provocation, which can alter the results.

Here we studied variability in the vocal activity of Boreal Owl based on acoustic monitoring using sound recorders. We predicted that the vocal activity of the Central European Boreal Owl would vary under a temporally variable environment (the year, the breeding season, and the hour of the night), weather conditions (wind speed and rain), and inter and intra specific competition (the occur-

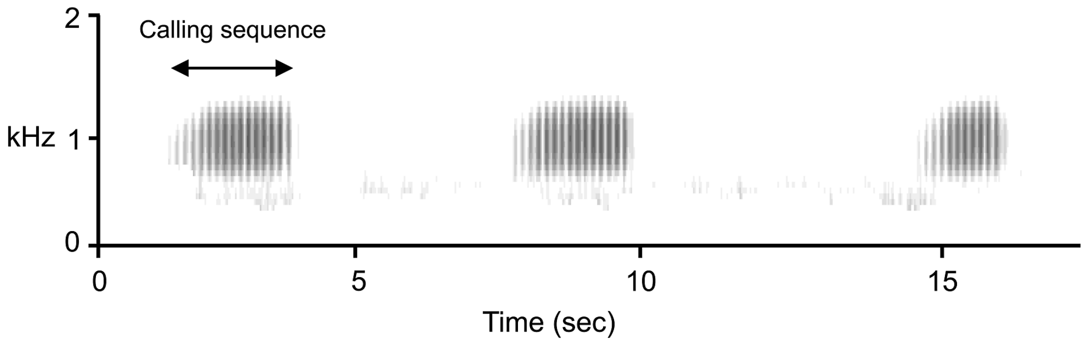

Fig. 1. The example of a spectrogram of Boreal Owl vocalization recorded in the Ore Mountains with one calling sequence indicated.

rence of Boreal Owl breeding pairs and the presence of other vocalizing owls). We also evaluated the vocal activity of other owl species to show its between-year and within-breeding season variability.

2. Methods

2.1. Study area and species

The study was conducted in the northern part of the Czech Republic (50° N, 13° E) on the Ore Mountain plateau (730–960 m a. s. l.; area 100 km^2) during the years 2015 and 2016. The study site was characterized by a heterogeneous mosaic of old forests of Norway Spruce (*Picea abies*), fragments of young secondary forests dominated by non-native Blue Spruce (*Picea pungens*), native deciduous trees (mainly European Beech *Fagus sylvatica*, European Larch *Larix decidua*, Rowan *Sorbus aucuparia*, European Hornbeam *Carpinus betulus*, alders *Alnus* spp., and birches *Betula* spp.), and open areas with solitary beech trees (Zárybnická *et al.* 2015c). Within the study site, Boreal Owls breed primarily in nest boxes (> 90% of nests) because the abundance of natural cavities is low, and breeding density used to reach to 10–30 pairs each year, depending on prey abundance (for details, see Zárybnická *et al.* 2015c).

2.2. Vocal activity of owls

Sound recorders (Olympus DM650) were installed within the study area during two periods. The first period took place between March 23 and April 1 and the second period between April 27 and May 4. All recorders were placed on "sampling points" located in a regular grid, 2 km from each other (radius 1 km) throughout the whole study area. Each recorder was placed on a tree trunk at a height of 1.5 m above the ground and left there for one night from 20:00 to 6:00 (i.e., 10 hours). During the period 2015–2016, we performed 144 recordings at 36 different sampling points, of which 13 recordings were not included in the analyses due to technical failures. For the first period (March 23–April 1), we analysed data from 34 and 36 sampling points in 2015 and 2016, respectively. For the second period (April 27–May 4), we used data from 26 and 35 sampling points in 2015 and 2016, respectively. Sound recordings were transformed to spectrograms (Fig. 1) and analysed using AMSrv software (Savický 2009). The spectrum was set at 1 min with FFT length and with a resolution of 4,096 and 1,366 window size. We used no filters to remove background noise.

We assessed the frequency of sampling points in which we recorded vocalizations of Boreal Owl and other owls (including Tawny Owl, Long-eared Owl *Asio otus*, Pygmy Owl *Glaucidium passerinum*, Eagle Owl *Bubo bubo*, and Little Owl *Athene noctua*) in relation to the year (2015, 2016) and recording period (March/April, April/May). The vocalization of each owl species was considered to be present when a specific territory call (based on bird voices in Kloubec *et al.* 2015) was detected at least once during the sampling period. We also analysed the duration of Boreal Owl vocal activity with associated variables being: year; recording period; the hour of the night (20:00–6:00);

wind speed (0–8.6 m/s); the presence/absence of rain; the presence/absence of other owl vocalizations; and the presence/absence of occupied Boreal Owl nest sites.

We defined the duration of Boreal Owl vocal activity as a sequence of continuous calling without a break (Fig. 1) and measured it as a total number of minutes of vocal activity per hour of recording. In total, 1,310 hours during 131 recordings at 36 sampling points were collected. For the purposes of the analyses, we excluded data with no Boreal Owl vocalization, meaning that we used 228 hours with Boreal Owl vocalization. We also used the presence/absence of vocalizations of other owl species during Boreal Owl vocalization. In particular, we included Tawny Owl and Long-eared Owl, which were detected during a total 35 and 11 hours of Boreal Owl vocalizations, respectively.

Other species (including Pygmy Owl, Eagle Owl and Little Owl) were not commonly detected during Boreal Owl vocalizations and thus they were not included in the analyses. We further used a presence/absence of occupied Boreal Owl nest sites (pairs) located in nest boxes within a radius of 1 km around each sampling point. We chose a 1 km radius because Boreal Owl vocal calling is usually detectable up to a distance of 1 km (Vacík 1991, Kloubec & Pačenovský 1996).

2.3. Prey abundance

Small mammal abundance is the main predictor of reproductive success of Boreal Owl in our study area (Zárybnická 2009a, Šindelář *et al.* 2015, Zárybnická *et al.* 2015a, d). We assessed the abundance of small mammals using snap-traps each year. Trapping was carried out each year at the beginning of June by setting up snap-traps in six areas (4 × 10 trap grid, span 10 m, 40 traps in total for each grid). The trapping points were evenly distributed throughout the study area (i.e., there is no detailed information on prey abundance for each sampling point). The traps were left out for three days and checked every morning. We calculated the abundance of small mammals as the number of captured individuals per 100 trap nights in each trapping area. All captured mammals (n = 19) were determined to species level.

2.4. Weather conditions

We used data on outdoor temperature (actual temperature in °C at each hour), rain (mm per hour), and wind speed (actual wind speed in m/s at each hour) from the Czech Hydrometeorological Institute. As the precipitation showed low variability (median = 0, SD = 0.16, min = 0, max = 1.9 mm/hour, n = 1310 hours), we used a binomial distribution for the presence/absence of rain (0/1) for the purposes of the statistical analyses. Mean wind speed and temperature reached 2.4 m/s (median = 1.9, min = 0, max = 8.6, n = 1310 hours) and 4.6 °C (median = 4.7, SD = 2.6, min = –0.8, max = 11.5, n = 1310 hours), respectively, and both factors negatively correlated to each other (Spearman Rank Correlations; r_s = –0.335, P < 0.001, 95% confidence intervals: lower –0.396, upper –0.271, n = 1310 hours). As wind speed is known as a limiting factor of Boreal Owl vocalization and its influence is more pronounced than that of temperature (Bondrup-Nielsen 1978, Mikkola 1983, Palmer 1987), we used the wind speed and we did not include the temperature in the analyses.

2.5. Statistical analyses

The between-year differences in the abundance of small mammals were calculated using non-parametric Wilcoxon Matched Pairs Test (StatSoft 2013). The comparisons of the frequencies of sampling points between years (2015 *vs*. 2016) and the recording periods (March/April *vs*. April/May) were analysed using Chi-square tests (StatSoft 2013). We applied Bonferroni correction for dependent tests within each species. The level of significance after Bonferroni correction was set to 0.025.

The effect of factors related to duration of Boreal Owl vocalization (dependent variable) was tested in R 3.4.4. software (R Development Core Team 2011) using multi-model inference approach (model.avg function in MuMIn package) (Anderson & Burnham 2002, Whittingham *et al.* 2006, Burnham *et al.* 2011) based on AIC differences. We used the following factors for building candidate GLMM models (glmer function in lme4 package): the year (2015, 2016), the recording period (March/April, April/May), the hour of the night (20:00–06:00 as a categorical variable), the

Table 1. The total number of sampling points, the number of sampling points with the occurrence of owl vocalizations, and the frequency of sampling points at which owl vocalization occurred. Owl vocalizations were documented using sound recorders in the Ore Mountains at the turn of March/April and April/May in 2015 and 2016.

1 = No. of points, 2 = No. of points with vocal, 3 = Frequency of vocal/point.

Owl species	2015						2016					
	March/April			April/May			March/April			April/May		
	1	2	3	1	2	3	1	2	3	1	2	3
Aegolius funereus	34	20	0.59	26	13	0.50	36	17	0.47	35	6	0.17
Strix aluco	34	14	0.41	26	10	0.38	36	17	0.47	35	14	0.40
Bubo bubo	34	0	0	26	0	0	36	1	0.03	35	0	0
Glaucidium passerinum	34	3	0.09	26	2	0.08	36	2	0.06	35	2	0.06
Asio otus	34	3	0.09	26	3	0.12	36	3	0.08	35	3	0.09
Athene noctua	34	0	0	26	0	0	36	1	0.03	35	0	0

absence/presence of rain (0–1), wind speed (m/s), the absence/presence of Tawny Owl (0–1) and Long-eared Owl vocalization (0–1), and the absence/presence of other breeding Boreal Owl pairs (0–1).

We built null and 32 alternative models with Gamma distribution of dependent variable and sampling point as a random intercept. We created these models with each individual factor and we consequently added temporal factors (the year, the recording period, and the hour of the night), weather factors (wind, rain), and inter-specific (occurrence of Tawny and Long-eared Owl vocalization) and intra-specific (occurrence of Boreal Owl breeding pairs) competition factors. We also tested interactions between temporal variables (year, recording period and hour). To validate our models, we checked for the pattern of residuals.

3. Results

The abundance of small mammals was significantly higher in 2015 (mean ± SD, 2.50 ± 1.18 ind./100 trap nights) than in 2016 (0.14 ± 0.34 ind./100 trap nights) (Z = 2.2, $P = 0.02$, $n = 6$). In 2015, we caught 18 small mammals: 11 Yellow-necked Mice (*Apodemus flavicollis*), 4 Bank Voles (*Myodes glareolus*), 2 Common Shrews (*Sorex araneus*) and 1 Common Vole (*Microtus arvalis*). In 2016, only one bank vole individual was caught.

The frequency of sampling points detecting vocalizations of Boreal Owls varied from 0.17 to 0.59, being higher at the turn of March/April compared to April/May (Chi = 5.0, $P = 0.025$) and being higher in 2015 compared to 2016 (Chi = 5.7, $P = 0.020$) (Table 1). The frequency of sampling points detecting vocalizations of Tawny Owl (min 0.38, max 0.47 per sampling point) was similar to Boreal Owl and stable between years (Chi = 0.2, $P = 0.700$), and it was higher at the turn of March/April compared to the turn of April/May (Chi = 5.7, $P = 0.021$) (Table 1). The frequency of sampling points detecting vocalizations of Long-eared Owl and Pygmy Owl was also stable between years (Chi = 0.130, $P = 0.718$; Chi = 0.528, $P = 0.467$) and during the breeding season (Chi = 0.087, $P = 0.768$; Chi = 0,528, $P = 0.467$), but it reached substantially lower values than Boreal and Tawny Owl (Table 1). At the turn of March/April in 2016, vocalizations of Eagle Owl and Little Owl were also recorded (Table 1).

The duration of vocal activity of Boreal Owl varied from 1 to 60 min per hour and from 1 to 230 min per night. Results of multi-model inference revealed that the interaction between years, recording periods and the hour of the night had the strongest effect on vocalization of Boreal Owl (Table 2, 3). The duration of vocal activity was higher late in the breeding season (April/May) compared to the early breeding season (March/April) in 2015, but this trend was not documented in 2016 (Fig. 2a–b). Further, an indicative effect of the hour of the night

Table 2. Set of candidate models used for multi-model inference. AIC values (AICc), changes of AIC (ΔAIC), and AIC weight (wi(AIC)) are shown. Abbreviations of factors: year (Y), recording period (P), hour (H), wind speed (WS), the occurrence of Long-eared Owl vocalization (OLV), Tawny Owl vocalization (OTV), Boreal Owl nesting pairs (OBN), and rain (R). Asterisks indicate the interaction of variables.

Model	*df*	AICc	ΔAIC	wi(AIC)
P*Y	6	1468.27	0.00	0.70
H+OLV+P+WS+Y	8	1473.61	5.34	0.05
H+OBN+P+WS+Y	8	1473.73	5.46	0.05
OLV+OBN+P+Y	7	1473.77	5.50	0.04
P	4	1474.24	5.97	0.04
OLV+OBN+P+WS+Y	8	1474.68	6.41	0.03
H+R+OTV+P+WS+Y	9	1475.83	7.56	0.02
OLV+OBN+OTV+P+WS+Y	9	1476.60	8.33	0.01
H*P	6	1476.87	8.60	0.01
H+OBN+OTV+P+WS	8	1476.93	8.66	0.01
Y	4	1477.11	8.84	0.01
H+OLV+R+OTV+P+WS+Y	10	1477.35	9.08	0.01
OLV+OBN+R+OTV+P+WS+Y	10	1477.73	9.46	0.01
H*Y	6	1477.99	9.72	0.01
H+OLV+OBN+R+OTV+P+WS+Y	11	1478.46	10.19	0.00
H+WS+Y	6	1479.04	10.77	0.00
H+OBN+Y	6	1479.12	10.85	0.00
OLV+OBN	5	1479.63	11.35	0.00
OLV+OBN+Y	6	1479.80	11.53	0.00
OBN	4	1479.81	11.53	0.00
H+OBN	5	1480.29	12.02	0.00
H+R+OTV+P+WS	8	1480.31	12.04	0.00
H+R+WS+Y	7	1480.69	12.41	0.00
OLV	4	1480.71	12.44	0.00
Null model	3	1480.90	12.63	0.00
R	4	1480.91	12.63	0.00
H	4	1481.04	12.77	0.00
H+R	5	1482.02	13.74	0.00
H+OLV+R+WS+Y	8	1482.02	13.75	0.00
WS	4	1482.05	13.78	0.00
OTV	4	1482.60	14.32	0.00
H+R+OTV	6	1483.27	14.99	0.00
H+R+OTV+WS	7	1485.14	16.87	0.00

was found (Table 2, 3). Two peaks of vocal activity were recorded between 23:00–24:00 and 03:00–04:00 (Fig. 2c). The effect of other variables (i.e. rain occurrence, wind speed, the presence of other Boreal Owl nesting pairs, Long-eared Owl vocalization, and Tawny Owl vocalization) was not significant (Table 2, 3).

4. Discussion

We found Boreal Owl and Tawny Owl were the most abundant species in our study area while Eagle Owl and Little Owl occurred rarely. The frequency of sampling points in which we recorded Boreal Owl vocal activity changed between years and within the breeding period. No such relationship was found in other owls, except for Tawny Owl in which the frequency of sampling points with vocalizations changed during the breeding period.

Boreal Owl vocalizations occurred at more sampling points at the turn of March/April compared to the turn of April/May. In Northern and Central Europe, a peak of vocal activity of Boreal Owl usually occurs during February/March and March/April, respectively (Mikkola 1983, Kloubec & Pačenovský 1996, Kloubec 2007, Korpimäki & Hakkarainen 2012). In our study, females initiated egg laying on average on April 21 (*SD* = 23 days, *n* = 58 nesting attempts, M. Zárybnická unpubl. data). As the vocal activity of owls usually decreases during egg laying, when individuals communicate using contact voices only (Lundberg 1980, Korpimäki 1981, Vacík 1991), we suggest the vocal activity of our Boreal Owls was probably reduced in the late breeding season because egg laying was already initiated.

On the other hand, the duration of Boreal Owl vocal activity showed the opposite trend; it increased at the turn of April/May compared to the turn of March/April in the year of high food abundance, but this trend was not found in the year of food scarcity. It has been documented that unpaired (bachelor) males usually call throughout the night or even during daytime later in the breeding season (Vacík 1991, Mrlík 1994, Kloubec & Pačenovský 1996, Korpimäki & Hakkarainen 2012). We recorded a similar situation in our study area in 2003 where a Boreal Owl male, after an unsuccessful nesting attempt due to predation by Pine Marten (*Martes martes*), intensively called during night and midday to find a new mate (M. Zárybnická unpubl. data). Therefore, we suggest more intensive Boreal Owl vocalizations presented at fewer sampling points in late breeding season could probably have resulted from increased activity of unpaired individuals.

We found that year explained both the frequency and duration of Boreal Owl vocal activity. Boreal Owl vocalization occurred at more sampling points and for a longer time in 2015 compared to 2016. We further found different food conditions between two years; the peak of Yellow-necked Mouse was in 2015 while a scarcity of both voles and mice occurred in 2016. It has been documented that the vocal activity of Boreal Owl increased with a higher number of breeding owl pairs (Kloubec & Pačenovský 1996) while the breeding density of Boreal Owl usually depends on the availability of small mammals (Korpimäki & Hakkarainen 2012). In particular, young and in-

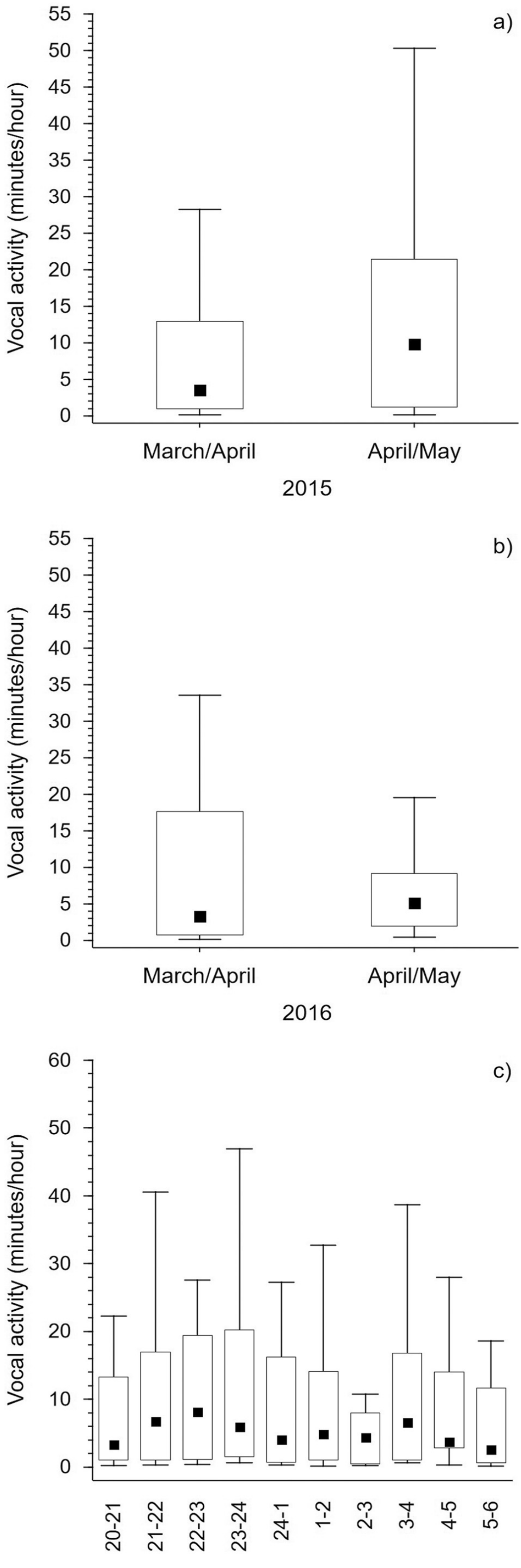

Fig. 2. The duration of Boreal Owl vocalization in relation to a) the year, b) the recording period (*P* = 0.018), and the hour of the night (*P* = 0.073). Box plots: median, range 25–75% of data, non-outlier range.

Table 3. The effect of particular factors on the duration of Boreal Owl vocalization based on full-model Multi-model inference. RVI – relative variable importance. Asterisks indicate the interaction of variables. Significant (P < 0.05) or indicative (P < 0.10) results are in bold.

Independent variables	RVI	Estimate	*z*	*P*
Intercept		1.654	4.969	**< 0.001**
Recording period	0.96	0.807	3.033	**0.002**
Year	0.93	–0.196	0.699	0.485
Recording period*Year	0.70	–0.947	2.362	**0.018**
Hour	0.18	–0.042	1.361	**0.073**
Wind (m/s)	0.16	–0.093	1.161	0.246
Long-eared Owl vocalization (0/1)	0.16	0.400	0.976	0.329
Neighbouring nest of Boreal Owl (0/1)	0.16	0.345	1.074	0.283
Tawny Owl vocalization (0/1)	0.06	0.162	0.620	0.535
Rain (0/1)	0.04	–0.309	0.763	0.446
Hour*Recording period	0.01	0.002	0.035	0.972
Hour*Year	0.01	0.067	1.166	0.244

experienced males used to breed in good food years while they do not breed during years of food scarcity (Korpimäki 1988). In our study area, between-year breeding densities of owls do not vary significantly (Zárybnická *et al.* 2013, Zárybnická *et al.* 2015a, Zárybnická *et al.* 2016).

However, the number of Boreal Owl nesting pairs was higher in 2015 compared to 2016 (34 *vs.* 24 breeding pairs, M. Zárybnická unpubl. data) suggesting that the vocal activity of Boreal Owl may differ significantly in years of extremely different food abundance. Similarly, Kloubec & Pačenovský (1996) documented a positive relationship between the frequency of vocalization in Boreal Owl and the number of prey items in food material collected from owl nests, and Palmer (1987) found a relationship between Boreal Owl vocal activity and prey abundance in North America. Swengel & Swengel (1995) revealed these relationships in Saw-whet Owl (*Aegolius acadicus*), and Lundberg (1980) found a positive relationship between the frequency of vocal activity in Ural Owl and vole abundance. Finally, we suggest the increased vocal activity of Boreal Owls in our study area probably resulted from increased density of breeding pairs as a result of the increased availability of small mammals.

In our study, Boreal Owls showed two peaks of vocal activity during the night, between 23:00–24:00 and 03:00–04:00, while they reduced its vocal activity between 24:00–03:00. Similarly, the vocal activity of Central European Boreal Owls, measured by vocal registrations (with vocal provocation by owls), dropped during midnight, and it also changed during the season (from March to May) in line with changing sunset and sunrise (Kloubec & Pačenovský 1996). Biphasic circadian rhythms of Central European Boreal Owl males, peaking during dusk and down were also documented based on the frequency of prey delivery to the nests (Klaus *et al.* 1975, Korpimäki 1981, Zárybnická *et al.* 2012). Similarly to males, Central European Boreal Owl females reduce their activities (measured as the frequency of departures from their nests during incubating and nestling period) between 23:00–03:00 (Drdáková-Zárybnická 2008).

Owl males can show monophasic patterns of activity when they increase the frequency of prey delivery to their nests during the nestling and fledgling phase (Zárybnická 2009b, Zárybnická *et al.* 2012) and/or during short nights in northern areas (Klaus *et al.* 1975, Korpimäki 1981, Zárybnická *et al.* 2012). We suggest the biphasic pattern of vocal activity of Boreal Owl males resulted from resting phases that males took between 24:00–03:00 h during long nights (taking around ten hours in April in Central Europe) and low hunting effort of non-breeding males.

Variability in Boreal Owl vocalizations can also result from other factors and particularly an individual and territorial quality that has been documented in Tawny (Appleby & Redpath 1997) and Eagle Owls (Penteriani *et al.* 2002, Penteriani 2003). Although Kloubec (1986) showed that the vocal activity of Boreal Owl tended to increase at localities with increased Boreal Owl densities, König *et al.* (1999) found that Boreal Owl can survive in a small area without the males being aggressive (10 breeding pairs/10 km^2). In our study, we were not able to identify individuals of calling Boreal Owls but we found the duration of Boreal Owl vocalizations did not significantly differ between localities with the absence or presence of Boreal Owl breeding pairs.

Owls are also frequently preyed on by other owl species and particularly smaller and weaker species may be taken as prey (Mikkola 1976). As a result, smaller and weaker species adjust their behaviour during the presence of competitors or predators. For example, the Little Owl reduced vocalization in the presence of its predator, the Barn Owl (*Tyto alba*) (Zuberogoitia *et al.* 2008), and a similar relationship was found between Tawny Owl and Eagle Owl (Lourenco *et al.* 2013). In our study, the vocalization of other owl species, namely Long-eared Owl and Tawny Owl, had no effect on the duration of Boreal Owl vocal activity. In particular, no inter-specific competition was revealed despite both Tawny and Boreal Owls greatly compete with each other for nest cavities (Petty 1989, Sunde *et al.* 2001, Korpimäki & Hakkarainen 2012), similar prey (Balciauskas & Balciauskiene 2014, Solonen *et al.* 2017, Yatsiuk & Filatova 2017), and habitats (Vrezec 2003, Vrezec & Tome 2004, Jensen *et al.* 2012). Since territories of Boreal and Tawny Owls can be highly segregated within habitats (Vrezec & Tome 2004) and across altitudes (Hudec *et al.* 2011, Flousek *et al.* 2015, Zárybnická *et al.* 2017), we suggest the absence of inter-specific competition could resulted from different space use of owl populations in our study site.

Finally, the presence of rain or wind speed had no effect on the duration of vocal activity of our Boreal Owls. Some authors have documented that strong wind speed, heavy rain, snow, and cloudiness reduce the vocal activity of owls, including Boreal Owl (Vacík 1991, Mrlík 1994, Kloubec & Pačenovský 1996, Lengagne & Slater 2002, Kloubec 2007). As a result, most authors avoided acoustic monitoring during unsuitable weather conditions (Freeman 2000, Galeotti & Sacchi 2001, Tripp & Otter 2006, Kissling *et al.* 2010). We suggest that the absence of heavy rains (the precipitations varied between 0.0 and 1.9 mm per hour in our data) and strong winds (reaching up to 8.6 m/s) has probably given cause for the missing effect of weather conditions on the vocal activity of our Boreal Owl.

We conclude that we have performed a rare study documenting the utilization of acoustic monitoring based on sound recorders in birds of prey with nocturnal activity, providing the basic methodology for further studies. We found that Boreal Owl vocalizations varied significantly between years, within breeding season (depending on food abundance), and over the course of the night. However, we did not confirm the effect of weather conditions, or inter- and intra- specific competition on the duration of Boreal Owl vocalization.

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Ympäristötekijöiden vaikutus helmipöllön ääntelyyn Keski-Euroopan populaatiossa.

Äänet mahdollistavat eläinpopulaatioiden paikallistamisen ja koon arvoinnin. Yksilöiden ääntelyaktiivisuuteen vaikuttavia tekijöitä on tutkittu hyvin vähän, varsinkin pöllöillä. Selvitimme ympäristötekijöiden vaikutusta helmipöllön ääntelyyn akustisella seurannalla Tsekissä Keski-Euroopassa (100 km^2 tutkimusalue).

Analysoimme 1 310 tuntia äänitteitä kahden kevään (2015 ja 2016, maalis–toukokuu) ajalta. Helmipöllöjä havaittiin 17–59 %:ssa havaintopisteistä. Havaintoja tehtiin enemmän vuosina, jolloin saaliseläimet olivat runsainpia (vuosi 2015), ja enemmän lisääntymiskauden alussa maalis–huhtikuussa. Ääntelyjakson kesto vaihteli 1–60 minuutin välillä: ääntelyjaksot olivat pidempiä lisääntymiskauden lopussa ja saaliiden huippuvuosina (2015). Yön aikana havaittiin kaksi korkeamman aktiivisuuden jaksoa. Sääolosuhteilla, muiden helmipöllöparien läheisyydellä tai muiden

pöllölajien ääntelyllä ei ollut vaikutusta helmipöllön ääntelyaktiivisuuteen.

Helmipöllön aktiivisuutta tutkittaessa on siis tärkeä ottaa huomioon sekä vuosien välinen, vuodenaikainen ja vuorokaudensisäinen vaihtelu. Tulostemme mukaan akustista seurantaa voidaan käyttää myös yöaktiivisten lintujen seurantaan.

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