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Flying or sleeping: flight activity of bats in natural cave with confirmed WNS

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Abstract. White-nose Syndrome (WNS) decimates bat populations in North America but similar effects have not been recorded in Europe. WNS-affected bats exhibit abnormal hibernation behaviour that prematurely deplete fat reserves and ultimately causes death by starvation. In the deep hibernation period (December–March) of 2006/07 (pre-WNS) and 2010/11 (post-WNS), we monitored bat hibernation behaviour and flight activity to test the potential impact of WNS on European bats. We registered no abnormal changes in bat hibernation behaviour (movement to visible sites, utilization of dynamic cave sections), flight activity level, its direction or seasonal pattern remained unchanged following WNS infection. Flight activity inside the cave and at its entrance was generally low during the deep hibernation period and temperature remained the best predictor of activity level. In general, stable hibernation behaviour and activity patterns suggests that they are apparently optimized for European winter conditions and support the hypothesis that the fungus has been present in Europe for a long time and has only recently invaded North America.

Key words: WNS, bat activity, hibernation behaviour, *Myotis myotis*, hibernacula

Introduction

Hibernation is a characteristic feature of the annual cycle of temperate zone bats and is an optimal energetic adaptation to a prolonged decline in ambient temperature and reduction in prey availability. Overwinter survival is influenced by many critical factors, including amount of stored energy, level and length of torpor, and hibernacula or microhabitat selection. While deep hibernation is interrupted by periods of arousal, which requires costly thermogenesis (internal heat production) (Thomas et al. 1990), flight activity of bats during arousals is minimal (Berková & Zukal 2006). Arousal may occur for a number of behavioural and physiological reasons, including switching of hibernation site, drinking, feeding (in mild periods or regions), excretion, or even mating (Zukal et al. 2005, Hope & Jones 2012). Regular arousal may also boost the immune system as hibernation is known to negatively affect the innate and adaptive immune systems (Bouma et al. 2010). These factors are not mutually exclusive, and the reason for arousal may depend largely on the ecology of a given species, its distribution and the local environment (Hope & Jones 2012).

A previous study on bat flight activity at the cave entrance showed a non-random temporal distribution

of activity shortly after the sunset. In general, flight activity remained nocturnal (between sunset and sunrise) and was associated with regular periods of arousal (Berková & Zukal 2006). Temperature appears to be the best exogenous predictor of the activity level and course of hibernation, the percentage of nights on which activity occurs during hibernation increasing with increasing temperature (Berková & Zukal 2010). Several bat species in North America and Europe are presently threatened by White-nose Syndrome (WNS). This new infectious disease was discovered in February 2006 in a cave in the north-east of the USA (Blehert et al. 2009, Puechmaille et al. 2011a) and is associated with a newly identified psychrophilic fungus *Pseudogymnoascus destructans* (Gargas et al. 2009, Kubátová et al. 2011). Since 2006 it has spread to caves throughout the eastern part of the USA. Hibernating bat populations at impacted localities have experienced dramatic population declines ranging from 30–100 % (Blehert et al. 2009, Frick et al. 2010). Presence of WNS was not confirmed in Europe prior to 2008, but has subsequently been identified at many localities from Portugal to Turkey (Puechmaille et al. 2011b, Pikula et al. 2012, Pavia-Cardoso et al. 2014, Pavlinic et al. 2015). In contrast with sites in North America, *P. destructans* in Europe

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does not appear to be associated with dramatic bat mortalities (Puechmaille et al. 2011a). In the Czech Republic, only slight population fluctuations have been observed in the most affected species, *Myotis myotis*, in accordance with the population trend predictions (Martínková et al. 2010).

WNS-affected bats typically have a visible white cover on the muzzles, nose, wings and ears (Courtin et al. 2010, Wibbelt et al. 2010), and exhibit abnormal hibernation behaviour that results in premature fat reserve depletion (Blehert et al. 2009, Boyles & Willis 2010, Puechmaille et al. 2011a). Abnormal behaviours included more frequent and unusual arousals during hibernation, winter day-flight activity, premature emergence from hibernacula, and roosting near entrances of hibernacula entrances (Hallam & Federico 2012, Reeder et al. 2012). The first *P. destructans* suspected bats are noted in January/February, but their number is the highest in March (Puechmaille et al. 2011b, Sachanowicz et al. 2014), when maximum number of hibernating *M. myotis* is observed.

Our objective was to test the influence of WNS on European bat hibernation behaviour and flight activity under natural conditions by repeating previous research at the same site carried out prior to WNS detection (Zukal et al. 2005, Berková & Zukal 2006, 2010), thus allowing a comparison between “unknown” (or unaffected) and WNS-affected stages of the bat community. We predict that if behaviour in European bats is affected by WNS, hibernating bats will exhibit abnormal flight activity (higher level and sooner onset) both inside the cave and at the cave entrance, respectively, and different hibernation patterns.

Material and Methods

Hibernation behaviour was studied at a regularly monitored natural limestone hibernaculum (Kateřinská cave, Czech Republic). Cave total length is around 500 m with one entrance that is closed by an iron gate with a vertical hole in its upper part (Berková & Zukal 2006). The cave consists of two main habitats, stable temperature sections and an outer (dynamic) section. Two species, *M. myotis* and *Rhinolophus hipposideros*, dominate the hibernating bat community, representing over 80 % of individuals. WNS-affected specimens (*M. myotis*) were first noted in the winter season 2008/09 even though intensive winter bat research had been conducted since 1992 (Zukal et al. 2005). WNS prevalence now approaches 2-3 % of hibernating bats (Horáček et al. 2014

and unpublished data). The presence of WNS was repeatedly confirmed by UV trans-illumination and histopathology (Turner et al. 2014, Zukal et al. 2014) in various bat species. Although *Myotis emarginatus*, *M. daubentonii*, *M. nattereri* and *M. bechsteinii* are rarely found hibernating inside the cave, they are dominant in netting samples from the cave entrance (Řehák et al. 1994).

The study was undertaken over two winter seasons before (2006/07) and after (2010/11) WNS outbreak. Only data from the „deep hibernation” period were analyzed, i.e. from mid-December to mid-March (Zukal et al. 2005). Seven biweekly observations were conducted, which included visual monitoring (no handling of hibernating bats minimizing any disturbance; Zukal et al. 2005) and observation of bat flight activity in the cave. Bat position was registered along with species present and clustering behaviour. Small species of *Myotis* genus i.e. all *Myotis* species with exception of *Myotis myotis* were pooled as *Myotis* sp. group as we were unable to determine all of them exactly. At the same days, flight activity inside the cave was observed using a Pathfinder 2000s night-vision scope one hour before sunset and two hour after sunset. The observer, sitting at narrow stairs separating the exit corridor from inner cave, recorded time and direction (IN vs. OUT) of each bat.

Bat movements through the gate hole were monitored continuously by a custom-made double infrared-light barrier connected to a data-logger. This system allows discrimination between bats leaving and those entering the cave (Berková & Zukal 2010), though species identification is not possible. After each bat passed the gate, time (hour and minute) and direction were stored by data-logger. As bats can fly in and out through the entrance hole several times, the number of bat passes will not always equal the number of active bats. However, this was used as a measure of activity entitled “emergence activity”. Reliable data were collected for 65 days pre-WNS and 79 post-WNS; these data being pooled into two-week periods for subsequent analyses.

Ambient outside temperature data were obtained from a weather station at Macocha abyss, 1.5 km from the study locality. An average of 24 hourly measurements was used for statistical analysis. The data logger malfunctioned between 21.2.2011 11:00 p.m. and 23.2.2011 9:00 p.m. due to extremely low temperatures.

Daily average temperatures for both sample seasons were compared using the t-test, while level of bat fluctuation during hibernation was evaluated using

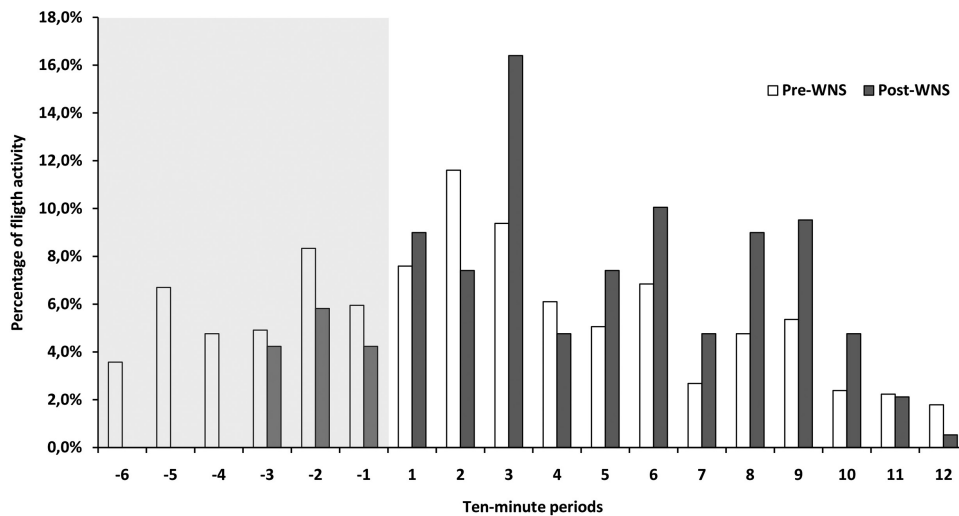


Fig. 1. The percentage of flight activity inside the cave during ten-minute periods. The periods before sunset are indicated by the grey area.

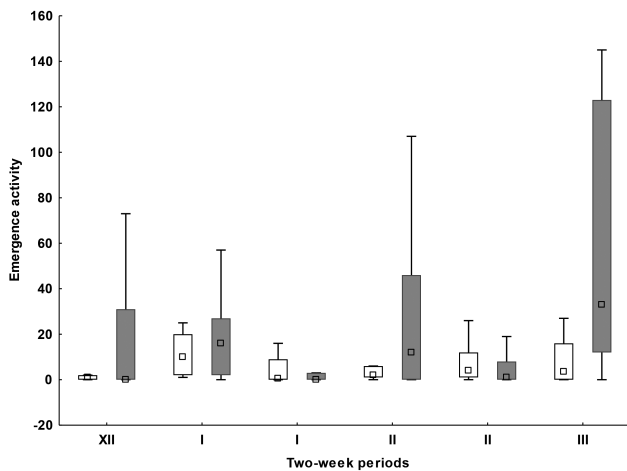


Fig. 2. Total level of emergence activity of bats at the cave entrance. Bat activity has not been affected by WNS and the bats did not leave the hibernaculum more often. Data pooled into two-week periods. Middle point, median; box, interquartile range; whisker, non-outlier range.

the Pearson Chi-square test. Nonparametric tests (Mann-Whitney U-test, Kruskal-Wallis ANOVA, Spearman correlation coefficient) were used for all other analyses as data could not be normalized. Two sided binomial test was calculated to compare the proportion of nights without bat activity. All statistical analyses were performed by Statistica for Windows 10.0 (Zar 1998).

Results

The highest numbers of hibernating *M. myotis* were registered near the end of deep hibernation in both seasons, though there were no statistically significant differences (Pearson Chi-square tests) in the model of bat number fluctuation (Table 1). *M. myotis* tended to move to dynamic parts of cave during winter, with their dominance in the hibernating bat guild increasing to nearly 50 %.

Table 1. Total number of bats, number of hibernating *M. myotis* registered during deep hibernation and their dominance in dynamic parts of cave during winter seasons.

Month	No. of bats		No. of <i>Myotis myotis</i>		<i>Myotis myotis</i>	
	Pre-WNS	Post-WNS	Pre-WNS	Post-WNS	Pre-WNS	Dynamic part Post-WNS
XII	138	104	31	23	38.7 %	47.8 %
XII/I	192	137	67	41	61.2 %	65.9 %
I	227	190	89	62	73.0 %	75.8 %
I	228	199	93	72	77.4 %	79.2 %
II	256	229	114	97	84.2 %	82.5 %
II	282	233	125	108	83.2 %	85.2 %
III	268	251	128	120	85.2 %	89.2 %
Pearson Chi-square test	5.019		4.724		0.008	
<i>p</i>	0.541		0.580		1.000	

Table 2. Parameters of bat flight activity registered by night vision scope inside the cave. Explanations: IN-OUT difference – the difference between the numbers of bats flying in deeper parts of cave and from this part to the corridor. Significant results ($p < 0.05$) are set in bold.

Month	Total level of activity		IN-OUT difference		Onset of activity after sunset		Median of activity after sunset	
	Pre-WNS	Post-WNS	Pre-WNS	Post-WNS	Pre-WNS	Post-WNS	Pre-WNS	Post-WNS
XII	19	14	1	0	–39	29	–4	32
XII/I	79	5	–3	–1	–53	–17	24	5
I	59	56	3	–2	–48	–18	36	34
I	63	58	1	0	–57	–29	8	26
II	99	3	1	–1	–43	26	43	26
II	157	0	7	0	–58		7	
III	196	53	–24	1	–60	–30	4	57
Mann-Whitney U test	3.0		15.5		0.0		13.0	
<i>p</i>	0.007		0.277		0.003		0.284	

Table 3. Results of Kruskal-Wallis ANOVA on the total level of emergence activity at the cave entrance and the ratio of IN vs. OUT flights during two seasons under study. Significant results ($p < 0.05$) are set in bold.

Month	Pre-WNS			Post-WNS		
	n	H	<i>p</i>	n	H	<i>p</i>
Total level of bat activity	65	29007	0.24	79	23.26	< 0.001
IN-OUT difference	65	19419	0.62	79	16.13	0.007

Flight activity inside the cave was low and onset was desynchronized i.e. starting before sunset (Fig. 1). Mean ambient temperature differed between winter seasons, with winter 2006/07 (before WNS) being significantly warmer (t-test, $t = 6.95$, $p < 0.001$, $df = 179$). During winter 2006/07, the activity started earlier and reached higher level; with highest activity noted during the first hour after sunset (Table 2). However, median flight activity and flight direction (IN vs. OUT) did not differ significantly between winters (Mann-Whitney test). General activity patterns, therefore, remained the same after the appearance of WNS.

Overall, there was no significant difference in the total level of emergence activity at the cave entrance (Mann-Whitney test, $z = 1.65$, $p = 0.10$, $n_1 = 65$, $n_2 = 79$) or the ratio of IN vs. OUT flights (Mann-Whitney test, $z = -0.01$, $p = 0.99$, $n_1 = 65$, $n_2 = 79$) between the two study seasons, i.e. bats did not leave the hibernaculum more often following outbreak of WNS (Fig. 2). Similarly, there was no difference in the proportion of nights with no emergence activity (Binomial test, $p = 0.43$, $n_1 = 65$, $n_2 = 79$). Total flight activity was correlated with mean ambient temperature (Spearman correlation, $r_s = 0.43$, $n = 65$, $p < 0.05$ in 2006 and $r_s = 0.90$, $n = 79$, $p < 0.05$ in 2010), which also influenced the overall course of emergence activity. Nevertheless, activity fluctuation

was higher during 2010/11 (Kruskal-Wallis ANOVA, Table 3), probably due to the colder winter.

Discussion

Since its discovery, WNS has killed millions of bats in northeastern USA and Canada. Such large-scale mortalities have not been documented in Europe, however, despite *P. destructans* being presently widespread (Martínková et al. 2010, Puechmaille et al. 2011b). This suggests that fungus may have been introduced to North America and European bats having developed immunity or evolved genetic or behavioural resistance to pathogen following historical exposure to *P. destructans* (Martínková et al. 2010, Puechmaille et al. 2011a, Leopardi et al. 2015). Moreover, previously published experimental study demonstrated that isolates of *P. destructans* from North America and Europe were both lethal to a North American bat species (Warnecke et al. 2012). In our study, we registered no abnormal changes in bat hibernation behaviour, activity level or its seasonal pattern after the WNS occurrence. Flight activity inside the cave and at its entrance was generally low during deep hibernation period and temperature remained the best predictor of activity level (Berková & Zúkal 2006, 2010). Higher ambient temperatures resulted in an increase in flight activity of bats and increasingly desynchronized activity onset, bats

leaving the cave even during January in some cases. Such activity patterns largely reflected the findings from *Rhinolophus ferrumequinum* studied by Park et al. (1999) at caves in south-west England. We believe, however, that winter cave emergence was caused by foraging activity of bats and not disturbance due to *P. destructans* infection, despite laboratory grown *P. destructans* showing optimal growth at temperatures typical in hibernacula; i.e. 3–15 °C (Gargas et al. 2009, Verant et al. 2012) and declines in *Myotis lucifugus* were higher in hibernacula with higher temperatures (Langwig et al. 2012). Increased flight activity under such conditions may be protective adaptation as it is always coupled with grooming behaviour that damages the fungus cover. The lack of a continual increase of prevalence of *P. destructans* suspected bats in late March was registered in an abandoned Polish ore mine and seems also to be related to increasing arousals and activity of bats (Sachanowicz et al. 2014). Nevertheless, the absence of visible white fungal growth on bats does not mean the lack of *P. destructans* infection.

Flight direction, movement to visible sites, utilization of dynamic cave sections, and emergence activity also remained unchanged following WNS infection, with activity patterns apparently optimized for European winter conditions (Fuszara et al. 1996, Zukal et al. 2005, Berková & Zukal 2006). Moreover, movement of bats to the colder and drier parts of cave may

result in a decline of *P. destructans* growth and such roosts will provide a refuge from disease (Langwig et al. 2012, Verant et al. 2012). This will be most important at the end of hibernation when European bats show high prevalence of infection (Martínková et al. 2010, Puechmaille et al. 2011a). Bats hibernating in colder outer spaces will save more fat stores for the rest of hibernation (Thomas et al. 1990, Boyles & McKechnie 2010).

Observed behavioural adaptations should help hibernating bats to survive pathogen attacks and they should be a result of previous evolutionary development when WNS acted as a strong selection force (Martínková et al. 2010). Therefore, low prevalence of WNS (2–3 % of bats) registered at the locality under study combined with stable hibernation behaviour support the hypothesis that the fungus has been present in Europe for a long time and has only recently invaded North America. Alternatively, low prevalence should bias our results as the expected behavioural changes cannot be detected under such conditions.

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