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Macroecological characteristics of bat geomycosis in the Czech Republic: results of five years of monitoring

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Abstract. Infestation of hibernating bats by infectious fungus *Geomyces* (*Pseudogymnoascus*) *destructans* (*GD*) was monitored in 13 regions of the Czech Republic from 2009 to 2014 using a standardized field protocol. Although fungus mycelia were recorded in 12 bat species, only two of them (*Myotis myotis*, in a smaller extent also *Myotis emarginatus*) were infested regularly. In total 20,268 individuals of *M. myotis* (by far the most infected species) were examined, 4047 of them being *GD* positive. The mean site positive rate varied among years from 61.3 to 71.2%, the mean total prevalence varied from 10.4 to 26.3% with considerable differences between particular regions (with total site positive rate 41.8–100%, and total prevalence 2.7–49.2%). Despite temporal variation, the pattern of geographic (inter-regional) variation remained unchanged throughout all five winters: mean regional values were low in lowland and karstic regions (site positive rate 20–42%, prevalence 0–7%), while in mountain and submontane hibernacula and/or those situated in a dynamic relief with stone debris cover and high surface humidity they were quite high (prevalence 22–58%, site positive rate 55–100%). Contrary to our expectations, we found no significant relation between prevalence of geomycosis and the abundance of hibernating populations or cluster size. The vast majority of observed cases showed the weakest stage of infection, severe damages (e.g. macroscopic lesions on auricles or wings) were rather exceptional. No case of mortality directly caused by *GD* was recorded. The pattern of prevalence does not suggest that *GD* is a specialized pathogen. The considerable difference between Europe and North America in mortality associated with the WNS and its possible causes (different tactics of hibernation, habituation to skin injuries due to high ectoparasite load in Europe etc.) are discussed.

WNS, Geomyces destructans, bats, Europe, macroecology, origin

Introduction

The white nose syndrome (WNS), a hypervirulent disease causing mass mortality of bats in the North American hibernacula, became a subject of intensive study soon after its first appearance in 2006 (Foley et al. 2010, Blehert 2012). The fungal growth on the face and skin surfaces of hibernating bats, after which the disease was named, was finally found, against expectancy, to be the sole pathogenic agent responsible for mass mortality in every hibernaculum where it appeared (Blehert et al. 2009). The fungus was identified as a close relative of *Geomyces pannorum*, the most common soil fungus in the Northern Hemisphere (Marshall 1998), and based on distinct morphological, genetic and physiological characters described as *Geomyces destructans* by Gargas et al. (2009). Specific characteristis of the fungus include a slow proliferation within a restricted thermal zone of 3–20 °C (with maximum activity around 14 °C) and mass production of curved heavy spores not capable of aerial dispersal. Infection of bats thus proceeds via physical contact.

Regarding these first pieces of information, we tentatively screened occurrence of fungal growth on hibernating bats in the Czech Republic during the winter 2008/2009 and found it at seven sites, at that time without exact identification of the fungus, of course. Yet, for the next winter we established a standardized monitoring project, supplementing the regular monitoring of hibernacula performed in the country since 1969 (Horáček 2010) with an additional March inspection specifically focused on the occurrence of fungus growth on bats. In the winter 2009/2010 we inspected 98 sites in the Czech Republic and Slovakia and in 76 of them we found infected bats. At the same time, the first proof of appearance of *Geomyces destructans* on European bats was reported from France (Puechmaille et al. 2010). The results obtained from the Czech Republic and Slovakia (then already supported by detailed molecular and microscopic identification confirming identity of the fungus with the American agent – Martínková et al. 2010) demonstrated its widespread distribution and *Myotis myotis* as its major host species. Yet, against expectancy, we found no case of mortality caused by the fungus nor any clear effects upon population trends, the fact later reported also from other European countries (Wibbelt et al. 2010, Puechmaille et al. 2011a, b). A retrospective analysis of randomly taken photographs of over 6000 hibernating bats revealed bats with fungal growths since 1995; however, the incidence of such bats increased in *Myotis myotis* from 2% in 2007 to 14% by 2010 (Martínková et al. 2010). Consequently, we expected an epizootic spreading in the next winters and decided to continue with the monitoring in further years.

Here we briefly report results of five years of the monitoring (2010–2014) with particular respect to temporal and geographic variation in appearance of macroscopically identified geomycosis (i.e. visible mycelia cover) in *Myotis myotis*, the only species regularly infected. The detailed analyses estimating effects of numerous environmental variables in particular roosts and other contextual factors are in progress and will be published elsewhere.

It should be remembered, of course, that since the time of the first record of *Geomyces destructans* in the Czech Republic and the beginning of the monitoring project, the information on various aspects of the WNS phenomenon has increased substantially (e.g. Meteyer at al. 2009, Reichard & Kunz 2009, Turner et al. 2009, Boyles & Willis 2010, Cryan et al. 2010, Frick et al. 2010, Fuller et al. 2011, Lorch et al. 2011, Meteyer et al. 2011, Flory et al. 2012, Meteyer at al. 2012, Wilder et al. 2011, Willis et al. 2011, Turner et al. in press). In Europe, the studies on geomycosis confirmed the identity of the WNS histopatological characteristics with the situation found in North America (Pikula et al. 2012), refined mycological characteristic of the fungus (Kubátová et al. 2011) and repeatedly confirmed surprising differences in pathogenic effects and mortality between North America and Europe (Martínková et al. 2010, Puechmeile et al. 2011a, b, Cryan et al. 2013a, Zukal et al. 2014).

The true background of the differences is largely unknown (Cryan et al. 2013a, b, Zukal et al. 2014), yet, it seems to be clear that the appearance of the fungus in Europe predates its first appearance in North America (Martínková et al. 2010, Puechmaille et al. 2011a, Lorch et al. 2013). Consequently, *GD* is considered to be a novel pathogen to North America, disseminated by incidental transport from Europe. This possibility was indicated by the genetic homogeneity of the North American fungus contrasting with its genetic variability in Europe (Martínková et al. 2010, Minnis & Lindner 2013) and, finally, proved by experimental infection of North American bats with the European fungus strains (Warnecke et al. 2012). Already for that reason, any data on the distributional pattern and macroecological characteristics of bat geomycosis in Europe might present an information of considerable significance.

Last but not least it should be remembered that a detailed molecular analysis revealed considerable diversity in the *Geomyces pannorum-destructans* clade, for which a new genus *Pseudo-*

Table 1. Synoptic survey of monitoring data for two most frequently *Geomyces destructans* infected bat species, *Myotis myotis* and *M. emarginatus*. Explanations: N reg, N sites – number of regions and sites in which the species was recorded, Mr+ and Tr+ – mean and total site positive rate, percentage of *G. destructans* positive localities, MP and TP – mean and total prevalence (percentage of *G. destructans* positive bats per locality), WNS+, *GD*+ – number of sites and bat individuals with a positive *G. destructans* record

year	N reg	N sites	WNS+	N ind.	*GD*+	Mr+	MP	Tr+	TP
Myotis myotis									
2010	12	66	47	3352	348	83.13	20.7	71.2	10.4
2011	13	93	62	3559	628	70.77	28.8	66.7	17.6
2012	13	119	73	4576	1205	66.62	24.9	61.3	26.3
2013	13	108	73	4390	1019	73.10	29.5	67.6	23.2
2014	10	101	67	4391	847	75.70	26.3	66.3	19.3
mean	12.2	97.4	64.4	4053.6	809.4	73.87	26.0	66.6	19.4
total	13	487	324	20268	4047	74.00	26.0	67.0	20.0
Myotis emarginatus									
2010	–			–	–				–
2011	5			355	31				8.73
2012	6			794	27				3.40
2013	4			486	8				1.65
2014	4			675	76				11.30
mean	4.75			577.5	35.5				6.15
total	–			2310	142				6.10

gymnoascus was erected (Minnis & Lindner 2013). Nevertheless, the reason for which the genus *Geomyces* should be split (genetic diversity of one of its branches) sounds not too convincing. For the moment we still hesitate to respect this opinion and in the present paper we continue to use the name in its traditional combination, i.e. *Geomyces destructans* Gargas, Trest, Christensen, Volk et Blehert, 2009 (further referred to as *GD*).

Material and Methods

The project of WNS monitoring in the Czech Republic was participated by the following persons who performed the field investigation and provided their data to a central database: T. Bartonička, L. Bufka, Z. Buřič, J. Červený, D. Duhonský, O. Fabiánek, L. Faltejsek, J. Flousek, V. Hanzal, D. Horáček, I. Horáček, H. Jahelková, M. Joža, J. Juda, V. Káňa, M. Kareš, M. Kašpar, M. Koudelka, M. Kovařík, M. Kubelka, R. Lučan, M. Maláč, J. Matějů, J. Neckářová, P. Schnitzerová, J. Šafář, P. Tájek, R. Vlček, Z. Vitáček, J. Veselý, J. Wagner, K. Weidinger, and J. Zukal.

The monitoring was undertaken in a form of standardized late February or March checks in major hibernacula representing 13 geographic regions: A – Český kras (Bohemian Karst), B – Jílové-Příbram region in Central Bohemia, C – Kokořín region, D – Jizerské hory Mts., E – Lužické and Krušné hory Mts., F – Šumava Mts., G – Krkonoše Mts. (Giant Mts.), H – Jeseníky Mts., I – Oderské vrchy Mts., J – Javořičko region, K – Moravský kras (Moravian Karst), L – Tišnov Karst, M – southern Moravia. In total 122 sites were included. Unfortunately, not all sites were inspected each winter – the mean number of inspected sites per year was 97, comp. Tables 1, 2.

Each inspection was focused on (i) a careful visual examination of all individual bats for macroscopic signs of *GD* mycelia, with no disturbance of the bats (except for contact sampling of mycelia for genetic and cultivation purposes in a minor part of infected bats). (ii) In each individual, the extent of mycelia cover was recorded using five categories: 0 – no signs of mycelia, 1 – indistinct sparse mycelia not specifically concentrated, 2 – distinct mycelia cover on the face or nose region, 3 – mycelia cover extending to other parts of the body, auricles etc., 4 – visible skin injuries supposedly caused by the geomycosis (lesion on auricles etc.).

The results were deposited in a central database, now including records from 497 inspections. The present summary dealing with this dataset provides a basic account of the distribution of positive *GD* records in the temporal and geographical respect, using two basic quantitative measures: site positive rate (percentage of sites with a positive record) and prevalence (percentage of infected *Myotis myotis* and/or *M. emarginatus* individuals), and basic statistics operating with them.

The term mean site positive rate / prevalence (Mr+, MP) refers to an average value of site positive rate /prevalence values in a set of single controls in the respective region or period, the term total site positive rate / prevalence (Tr+, TP) refers to percentages calculated from the total number of sites/individuals inspected and number of *GD* positive sites/individuals in the respective region or period. The contextual variables used in the present analyses were restricted to altitudinal zone (<200, 200–400, 401–600, 601–800, >800 m a. s. l.) and rock substrate (limestone, sandstone, crystalline/metamorphic rocks). Host-aspect variables included bat species, abundance in a site/region, and cluster size where it was reported.

The effects of particular factors upon site positive rate and prevalence (as dependent variables) were examined using ANOVA (univariate results with sigma-restricted parametrization) and a mixed ANOVA/ANCOVA model used for the comparison of roles of particular factors. Computations were undertaken with the Statistica 8 software.

Results

The monitoring revealed appearance of the geomycosis (mycelia growth of *Geomyces destructans* confirmed by microscopic identification of spores) in 12 bat species (Table 3). Yet, only in *Myotis myotis* its occurrence can be characterized as regular and widespread – it made up 94.2% of all

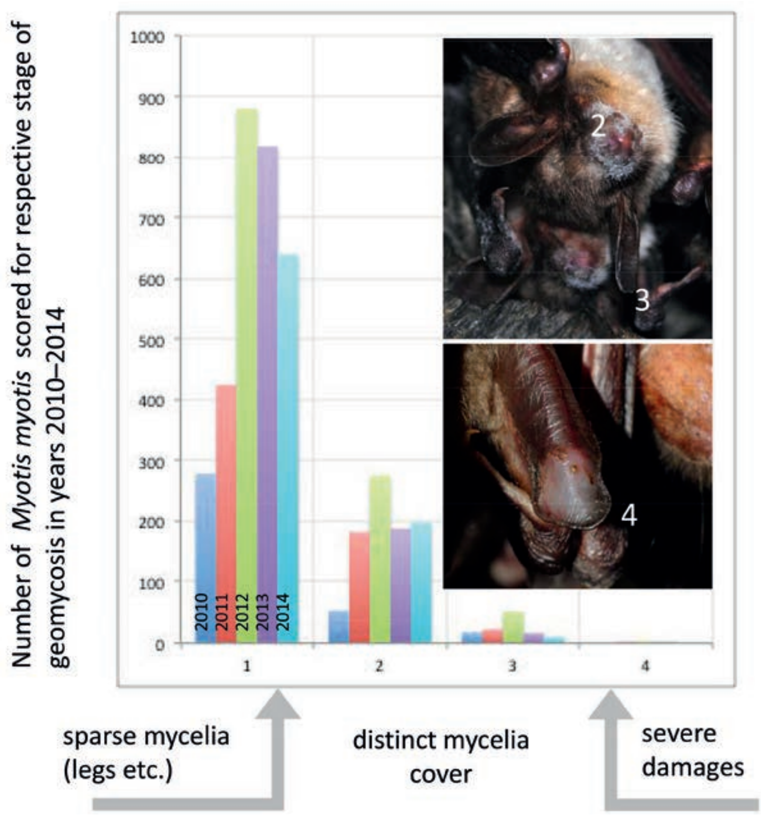

Fig. 1. Total numbers of *Myotis myotis* individuals scored for particular stages of *Geomyces destructans* mycelia growth during late February/March checks in the winters 2010–2014.

Table 2. General survey of the monitoring record: list of mean values of *Geomyces destructans* site positive rate and prevalence in particular regions and winters and their basic statistics. M – mean, N – number, T – total

region	A	B	C	D	E	F	G	H	I	J	K	L	M
site-positive rate													
2010	33.0	42.9	100.0	77.8	80.0	100.0	100.0	63.6	100.0	100.0	100.0	100.0	–
2011	42.9	46.7	50.0	53.9	66.7	100.0	100.0	100.0	90.0	50.0	70.0	100.0	50.0
2012	43.8	42.9	50.0	54.6	80.0	100.0	85.7	69.2	65.0	100.0	100.0	25.0	50.0
2013	27.3	72.7	33.3	88.9	100.0	100.0	75.0	58.3	55.0	100.0	66.7	100.0	–
2014	37.5	36.8	–	63.6	60.0	100.0	100.0	100.0	81.3	100.0	77.8	–	–
M	36.9	48.4	58.3	67.7	77.3	100.0	92.1	78.2	78.3	90.0	82.9	81.3	50.0
min	27.3	36.8	33.3	53.9	60.0	100.0	75.0	58.3	55.0	50.0	66.7	25.0	50.
max	43.8	72.7	100.0	88.9	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	50.0
SD	6.9	14.1	28.9	15.3	15.4		11.4	20.2	18.3	22.4	16.1	37.5	0
prevalence													
2010	3.2	19.4	23.8	39.3	19.5	5.0	56.5	15.8	29.1	14.3	1.9	20.0	–
2011	1.6	10.1	25.0	42.1	45.8	19.6	51.1	50.1	34.6	25.0	2.6	50.0	16.7
2012	5.4	21.4	20.0	47.3	47.3	33.3	24.1	54.8	28.0	20.8	3.2	3.3	14.3
2013	2.5	13.9	28.6	53.1	64.0	52.1	30.8	47.3	23.7	17.9	3.2	16.7	–
2014	2.8	14.2	–	33.1	36.7	52.4	25.1	47.9	20.8	27.0	2.9	–	
M	3.1	15.8	24.4	43.0	42.7	32.5	37.5	43.2	27.2	21.0	2.8	22.5	15.5
min	1.6	10.1	20.0	33.1	19.5	5.0	24.1	15.8	20.8	14.3	1.9	3.3	14.3
max	5.4	21.4	28.6	53.0	64.0	52.4	56.5	54.8	34.6	27.0	3.3	50.0	16.7
SD	1.4	4.6	3.5	7.6	16.3	20.6	15.2	15.6	5.3	5.2	0.6	19.7	1.7
M sites	11.0	14.6	2.0	16.8	6.4	3.8	6.0	9.0	16.6	2.2	7.0	2.0	2.0
M sites+	4.6	6.8	1.0	11.2	4.8	3.8	5.2	6.4	12.4	2.0	5.4	1.2	1.0
T t-p rate	41.8	46.6	50.0	66.7	75.0	100.0	86.7	71.1	74.7	90.9	77.1	60.0	50.0
N *M. myotis*	5071	761	45	1923	582	620	827	3186	1559	137	5483	61	13
WNS+	155	119	11	833	241	199	317	1567	415	30	147	11	2
Tr+	3.1	15.6	24.4	43.3	41.4	32.1	38.3	49.2	26.6	21.9	2.7	18.0	15.4

positive records (N=4298). Except for *Myotis emarginatus* (regularly infected at several sites in northern Moravia) and *Rhinolophus hipposideros* (not completely confirmed by microscopic identification), only single records per species were registered.

In *M. myotis*, both mean site positive rate and prevalence were very high: 73.87±5.51% and 26.0±3.15%. Overall, 66.6±9.62% of all sites and 19.4±5.41% of all checked individuals were *GD* positive. In most instances, initial stages (sparse mycelia growth) predominated in all winters and no clear trend towards more acute development was recorded (Fig. 1). The summary values for particular winters (Table 2) indicated an increasing trend in total prevalence during the first three years of the monitoring, however, further years revealed a rather opposite trend while the mean prevalence and mean site positive rate exhibited a distinct development. Correspondingly, the statistical analyses (Table 4) show no significant effects of temporal factors upon the state of either the site positive rate or prevalence. Surprisingly, the same results were obtained also for the number of sites examined in particular regions and years as well as for the number of bats, including abundance in particular hibernacula. At several sites from where data on cluster sizes and appearance of *GD*-positive bats in clusters were available, no significant correlation (Spearman r_S= –0.557, p>0.05 NS) was found between cluster size and prevalence of geomycosis.

The basic data on annual variation of the site positive rate and prevalence of geomycosis in *M. myotis* in different regions are summarized in Table 1. In contrast to temporal and abundance

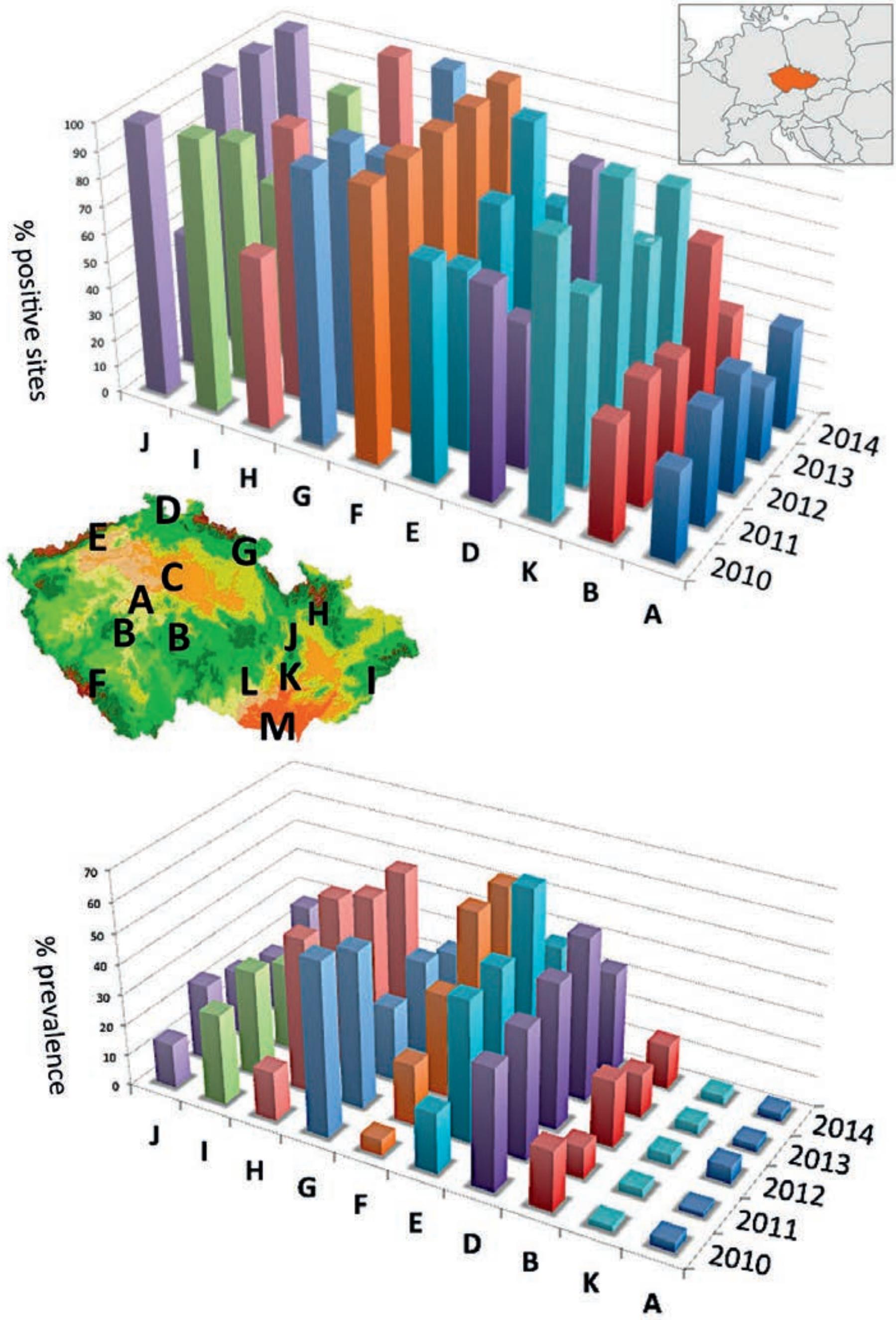

Fig. 2. A graphical survey of mean percentages of *Geomyces destructans* positive sites (top) and prevalence (below) recorded at late February – March checks in winter 2010–2014 in particular regions of the Czech Republic.

Table 3. List of bat species with a positive record of *Geomyces destructans* (*GD*+) and the respective number of infected individuals in the monitoring record (Czech Bat Conservation Trust, ČESON) and in further data reported from the Czech Republic by Zukal et al. (2014)

source	ČESON records		Zukal et al. (2014)	
bat species	*GD*+	prevalence	*GD*+	prevalence
Myotis myotis	4047	0.20	37	0.55
Myotis emarginatus	142	0.06	5	0.13
Rhinolophus hipposideros	67	0.02	1	0.04
Myotis mystacinus	22	0.11	–	–
Plecotus auritus	6	0.08	5	0.22
Myotis daubentonii	6	0.01	4	0.16
Myotis brandtii	3	0.03	1	0.06
Myotis bechsteinii	1	0.10	2	0.10
Myotis dasycneme	1	0.25	1	1.00
Eptesicus nilssonii	1	0.01	1	0.25
Plecotus austriacus	1	0.25	0	0.00
Myotis nattereri	1	0.01	3	0.15
Barbastella barbastellus	0	0.00	3	0.18

variables, the effect of region and its geographic setting (altitudinal zone, rock substrate) were found to be significant factors responsible particularly for prevalence (Table 4). In comparison to this, the site positive rate of geomycosis shows significant effects of inter-regional differences, while the effects of altitude and rock substrate are much less pronounced. A mixed ANOVA/ANCOVA model indicated a prevailing effect of altitudinal zone ($F=36.140$, $p<0.001$) over rock substrate ($F=9.611$, $p=0.003$) and region ($F=3.398$, $p=0.002$) upon *GD* prevalence (with similar but much less distinct scaling in the case of *GD* site positive rate), which is in good agreement with a basic comparison of individual regions concerning the total prevalence and total site positive rate values (Fig. 2). While in karst regions situated in the medium altitude zone (A, K) the *GD* prevalence was very low, in mountain regions both prevalence and site positive rate showed extreme values (Fig. 3).

Discussion

First of all we feel obliged to discuss the question whether and/or to what degree the appearance of macroscopic mycelia on bat skin surface, i.e. the subject of the screening within the present

Table 4. Univariate results of ANOVA analyses on the effects of particular contextual variables (number of sites, number of *Myotis myotis* individuals, years, regions, altitudinal zone and rock substrate) upon mean values of *Geomyces destructans* site positive rate and prevalence in total dataset

factor	site-positive rate		prevalence	
	F	P	F	P
N sites	1.499	0.139 NS	1.283	0.247 NS
N *Myotis myotis*	0.601	0.853 NS	1.282	0.247 NS
year	1.281	0.289 NS	0.483	0.749 NS
region	3.711	0.006**	6.994	0.001***
altitudinal zone	3.794	0.016*	16.565	0.001***
rock substrate	1.255	0.283 NS	16.721	0.001***

project, provides a relevant information on the actual extent of infestation of bats by *Geomyces destructans*, and, hence, what is the actual meaning of the data surveyed in this report. Zukal et al. (2014) demonstrated that a considerable part of bats leaving hibernacula in early spring were *GD* positive in regard to appearance of minute skin lesion visible under UV-illumination, their histopathological characters and identification of *GD* with the aid of microscopic and genetic analyses, however, in most instances, these bats showed no macroscopically visible fungal growth. This fact is in a good agreement with conspicuous decrease in number of bats with fungus growths observed by the end of hibernation period (end of March, April) in more monitored sites as well as with multiple observation of arousal behaviour of infected bats in that time which starts with extensive grooming behaviour removing all surface mycelia growth. Thus, it seems that appearance of macroscopically visible mycelia growth indicates a subacute stage of infection still not responded by arousal and its active removal. In this respect, the time frame of the monitoring seems to cover the period when fungus growth reached already its full development but still not evoked arousal in a considerable part of the infected bats. The values of site positive rate and prevalence obtained during that period can be thus looked upon as reliable at least for the purposes of between-sites and inter-annual comparisons.

The mean prevalence values reported by Zukal et al. (2014) are roughly twice higher than the respective species-specific values indicated by our visual monitoring results (Table 1). Yet the major patterns (e.g. *M. myotis* as far the most infected species) remain the same what also support relevance of the monitoring data. In regard to these facts we are convinced that the data surveyed in this paper are not essentially biased and are sufficient for reliable between-region and between-year comparisons.

The respective comparisons revealed (i) no clear temporal trends in either the site positive rate or prevalence of bat geomycosis in underground hibernacula of the Czech Republic, (ii) no trends towards a more acute development, (iii) no mortality effects, and (iv) no effects upon abundance

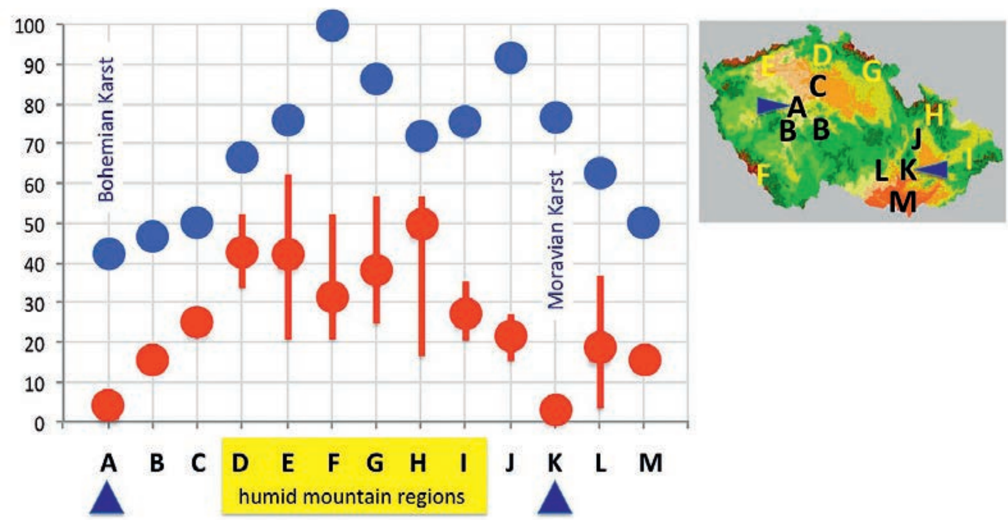

Fig. 3. Mean percentages of *Geomyces destructans* positive sites (blue dots) and prevalence (red dots) in particular regions of the Czech Republic over the whole period of monitoring (2010–2014).

trends in the particular hibernacula. In contrast, we found (v) highly significant interregional differences invariant to temporal variation, correlated with altitudinal characteristics and rock substrate. Against expectancy, we found neither relations between prevalence of the geomycosis and abundance of bats in a hibernaculum, nor a relation between prevalence and cluster size - the prevalence thus seems to be highest in solitary individuals and/or smaller groups. In this respect, the situation in the Czech Republic differs essentially from that in North America where the *GD*-prevalence shows a significant density-dependent pattern (Langwig et al. 2012).

In agreement with conclusions by Zukal et al (2014), neither the pattern of *GD*-prevalence in Central Europe revealed by our monitoring results suggests that *GD* is a specialized pathogen. The lack of relations of prevalence and site positive rate to host-aspect variables (including epizootic dynamics) and the greatly pronounced dependence upon abiotic context indicate that *GD* interferes with bats on a more or less incidental and non-targetted basis. Yet, with such conclusion, the story grew even more intricate. What would then be the true origin of the fungus and which are the factors establishing its interaction with bats, and why does it cause the mass mortality of several millions of American bats?

Our analyses revealed higher altitude and crystalline or metamorphic rock substrate as the most significant factors related to the high site positive rate and prevalence of the geomycosis. The combination of these factors is pertinent for the landscapes with extensive relief dynamics and appearance of thick subsurface scree deposits. Such deposits are quite common in many medium- to high-altitude regions of Central Europe (Raška et al. 2011) and form a specific habitat characterized by low internal temperature varying from –5 to 15 °C and rich invertebrate communities with a number of paleoendemic relic taxa (Růžička & Zacharda 2010, Růžička et al. 2012). The possibility that *Geomyces destructans* is, as well as its congeners, essentially an edaphic fungus specifically adapted to deep scree habitats (comp. its temperature requirements – e.g. Verant et al. 2012, contact dispersal of spores), seems to be in good accordance in this respect. It can be further hypothesized that warming episodes when the surface layers of scree deposits do not freeze in winter might promote dispersion of the fungus into wider surroundings including underground bat hibernacula. The fact that the major host species in Europe, *Myotis myotis*, is a specialized ground gleaner and initial stages of mycelia growth typically appear on its legs and thumb region of the forearms, is also worth mentioning in these connections.

The difference between Europe and North America in the effects of the geomycosis upon hibernating bats – with regard to genetic identity of the agent and/or identical histopathological characteristics of the infection (Pikula et al. 2012), the most striking aspects of the topic – is generally explained by a specific immune response in European bats induced by the effects of repeated previous exposures (Martínková et al. 2010, Puechmeille et al. 2011, Cryan et al. 2013b). However, despite intensive investigation, no convincing support for that hypothesis has been obtained so far, to our knowledge. Already for that reason a careful re-examination of other possible factors seems to be quite important. One of them might be related to the tactics of hibernation. Very large clusters formed regularly in mass hibernacula seem to be clearly a prevailing mode in the most affected American species (*Myotis lucifugus* in particular). On the other hand, Central-European bats hibernating in underground spaces are characterized rather by the solitary mode of hibernation and dispersal of the population into a large number of winter roosts including sites obviously far from ideal conditions. For *M. myotis*, this was entirely true in the 1960s–1980s at the time of relatively low abundances (comp. Horáček 1985), while the tendencies to form mass aggregations in optimal hibernacula have become apparent only with the abrupt increase in population numbers of this species during recent decades (Horáček 2010). Yet, even now, the majority of its population hibernates rather solitarily.

The ultimate cause of WNS mortality in North America (notwithstanding a number of proximate factors such as evaporative water loss and electrolyte imbalance due to skin injuries) is associated with repeated arousal due to the stress from skin injuries and rapid depletion of fat reserves (Warnecke et al. 2012, Reeder et al. 2013, Warnecke et al. 2013). Arousal of multiple individuals in a large cluster can produce a domino effect (Turner et al. in press) and disturb the essential advantages of that hibernation tactics – a long-term socially controlled thermal homeostasis of the cluster (Boyles et al 2008). The prevailing solitary tactics of hibernation of bats in Europe thus might be driven by repeated past exposures of bats to temporal presence of a certain disturbing agent in the hibernacula (e.g. *GD*) and can essentially reduce the danger of unintentional arousal by the grooming activity of neighboring individuals.

Yet, there is also another factor not taken into account so far. In comparison to Europe, the ectoparasite load in North American bats seems to be quite low: for instance, Poissant & Broders (2008) examined 1641 individuals of *Myotis lucifugus* and 417 individuals of *Myotis septentrionalis* and found only 317 individuals of *Spinturnix* mites, which means the prevalence of any ectoparasites was 16–25% and 26–34% in the former and the latter species, respectively. For the same species in swarming places, Czenze & Broders (2011) reported ectoparasite prevalence values 46% and 48%, respectively, and mean intensities of mite infestation in juveniles reaching 0.3 and 1.3, respectively. Webber et al. (in press) reported mite prevelance 23.9% with the overall intensity 0.44 for breeding colonies of *M. lucifugus*. In contrast, large breeding colonies of *M. myotis* in Central Europe suffer from an enormously high ectoparasite load of *Cimex* spp. and *Spinturnix myoti* with the prevalence not rarely amounting to 100% (Dusbábek 1972, Christe et al. 2000), typically with more than 10 mites on adult female and even much more on juvenile bat (Christe et al. 2000).

A corresponding situation was reported also for other European species (e.g. Zahn & Rupp 2004, Lučan 2006). Giorgi et al. (2001) measured energetic cost of the respective parasite loads and concluded that mites greatly affected time and energy budgets of bats in a colony. They caused increased grooming activity, reduced the overall time spent at rest and provoked a dramatic shortening of the rest bout duration. It seems very probable that European bats respond to such conditions with extensive habituation to the stress resulting from surface skin injuries, and their sensitivity to minute lesions caused by other agents, such as *Geomyces*, and thus also the danger of unintentional arousal, is much reduced in comparison to their American congeners. This possibility is worth of further examination.

In any case, the phenomenon of bat geomycosis, WNS, its origin and etiology as well as the striking differences in effects of the same agent on bats in different parts of the world present undoubtedly a very complicated and complex topic worth of intensive multidisciplinary study. We believe that the results of five years of WNS monitoring in the Czech Republic contributed to this issue in a useful way. Our study has excluded initial expectations of epizootic dynamics and the possibility of a real danger for local bat populations. In this respect it responded the claim of integration of scientific and conservation regards in the study of European bats, which was introduced into practice and steadily performed by the founding personality of modern bat research, the late Jiří Gaisler. We ascribe this paper to his memory.

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