Research Article

How winter prevailing weather conditions influence the bat activity patterns? Hints from a Mediterranean region

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Abstract

All mammalian hibernators arouse periodically throughout the winter and weather change conditions is one of the major drivers affecting their behaviour, phenology and distribution patterns worldwide, with potentially severe implications for biodiversity conservation. Although the relationships between bat distribution and prevailing environmental conditions are relatively well-known, the behaviour adaptation responses to scenarios of weather change conditions are still largely unknown. Temperate insectivorous bats show different ecological requirements for winter activity and bouts frequency depending on the species and weather prevailing condition. The European free-tailed bat (*Tadarida teniotis*) is a non-strictly hibernating bat species, characterized by short periods of torpor in contrast with other species from the Vespertilionidae and Rhinolophidae families, which are strictly hibernating bat species. This study was carried out in a Mediterranean region providing unique information on daily winter bat activity patterns with relevance for the understanding how instantaneous and cumulative weather conditions influenced non-strictly and strictly hibernating bat species winter activity patterns to anticipate ecological consequences under future climate change scenarios. Our results clearly demonstrate that instantaneous and cumulative weather conditions induce different behavioural responses on non-strictly and strictly hibernating bat species concerning winter activity, highlighting the importance of cumulative weather conditions for strictly hibernating bat species. Therefore, the understanding of the role of behavioural plasticity among bat communities to cope with changing weather conditions is critical, particularly for the activity patterns of the strictly hibernating bat species during hibernation. This is fundamental to anticipate the potential ecological consequences and the main challenges and priorities for bat conservation.

Introduction

All mammalian hibernators arouse periodically throughout the winter (Willis et al., 2006), which is typically associated with seasonal and specific variable biological requirements (Newton, 2008; Holte et al., 2017). Temperate insectivorous bats show different phenological requirements between breeding and hibernation seasons. They hibernate to overcome food scarcity induced by low ambient temperatures (Frick et al., 2010; Bellamy and Altringham, 2015), and to preserve energy when little or no food is available (Dunbar and Brigham, 2010; Miková et al., 2013). Environmental temperature influences thermoregulatory bat behaviour and hibernation traits (Dunbar and Brigham, 2010; Stawski and Geiser, 2011). The rate of depletion of energy reserves through the hibernation period is determined by the temperature-dependent metabolic rate and winter torpor, which consists of discrete torpor bouts separated by brief periods of normothermy or arousal behaviour (Thomas and Geiser; Luis and Hudson, 2006). Bat winter activity is relatively common and the activity patterns vary among species (Boyles et al., 2006; Johnson et al., 2012) and bouts frequency can vary between days or weeks, depending on the species and weather prevailing conditions (Park et al., 2000). Together, the timing, duration and frequency of arousals are critically important factors to the individuals' energy budget, in which the balance between the energetic benefits from torpor and also the costs of arousals must be

met (Humphries et al., 2003; Boyles et al., 2008; Jonasson and Willis, 2011).

Although the relationships between bat distribution and the prevailing environmental conditions are relatively well-known, the adaptation behaviour due to temperature increases and food availability in the winter season is still largely unknown. In temperate regions, bat activity pattern is relatively common throughout the year. As expected, their activity shows lower levels in autumn/winter when compared to spring/summer. Winter activity seems to occur mainly on occasional nights with milder weather conditions (Hays et al., 1992; Perry, 2012; White et al., 2014; Lemen et al., 2016). This apparent correlation between weather conditions and bat arousal is supported by a large number of studies (Klüg-Baerwald et al., 2016; Zahn and Kriner, 2016; Barros et al., 2017; Bartonicka et al., 2017).

The wintering behaviour patterns are critically important to the bats' energy budget balance (Jonasson and Willis, 2011) and differ from species to species. The European free-tailed bat (*Tadarida teniotis*) is the only Palaearctic species from the family Molossidae, exhibiting a somewhat unusual thermal behaviour, as expected from a representative of a mostly tropical family living in a temperate zone (Arlettaz et al., 2000). *Tadarida teniotis* is a non-strictly hibernating bat species (NSHBS), characterized by short periods of torpor under adverse weather conditions (Ibáñez and Pérez-Jordá, 1998). In fact, the *Tadarida teniotis* arousal frequency in winter seems to be relatively high compared to other species from the Vespertilionidae and Rhinolophidae families, which are strictly hibernating bat species (SHBS)
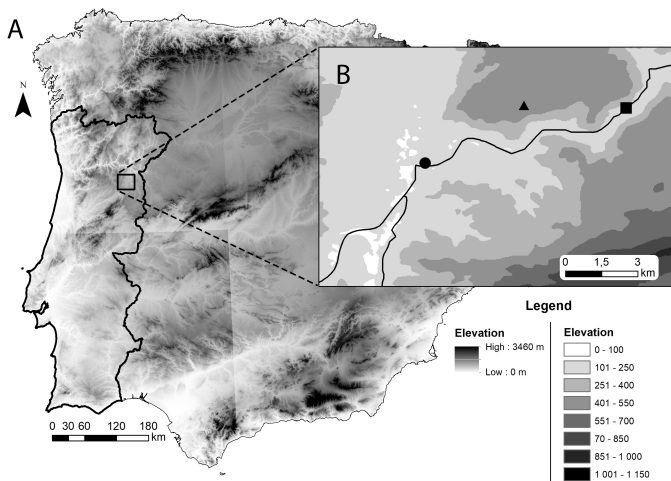
Figure 1 – Study area geographical location in northern Portugal (A), the acoustic sampling sites (B - square: upstream sampling site; circle: downstream sampling site) and the weather station site (B - triangle).

(Arlettaz et al., 2000). However, emerging changes in arousal behaviour patterns should be considered also as possible for SHBS from southern Europe in response to climate change.

Global climate change is one of the major processes affecting animal distribution worldwide, with critical implications for biodiversity conservation (Buckley and Jetz, 2007; Van Dyck, 2012; Tulloch et al., 2015). Climate change observed in recent decades has been expressed as a global increase in average air temperature of approximately 0.85 °C, over the period between 1880 and 2012 (Tomczyk et al., 2019). Nonetheless, besides the increase in global mean air temperature, local and regional warming can be substantially different from these global figures, particularly over continental areas in the Northern Hemisphere. Furthermore, climate change is associated with significant changes in many other variables, such as precipitation, wind, radiation and humidity. In this context, human activities are estimated to have caused approximately 1.0 °C of global warming above pre-industrial levels, with a likely range of 0.8 °C to 1.2 °C (IPCC, 2018). Global warming is likely to reach 1.5 °C between 2030 and 2052 if it continues to increase at the current rate (IPCC, 2014, 2018). Climate change is also manifested by the higher frequency, intensity and duration of extreme weather and climate events in many regions of Europe and around the globe (Diffenbaugh et al., 2017; Ummenhofer and Meehl, 2017), such as summertime heatwaves and wintertime warm spells (Tomczyk et al., 2019), which are widely recognized as having substantial impacts on terrestrial ecosystems (Reichstein et al., 2013). Several previous studies highlight that the recent past warming and drying trends over Portugal are projected to strengthen under future anthropogenic radiative forcing scenarios (Andrade et al., 2014; Santos et al., 2017, 2019).

Due to their high mobility, bats can respond rapidly to environmental changes (Jones et al., 2009) and, thus, climate change is expected to have a strong influence on bats' distribution (Sachanowicz et al., 2006; Lundy et al., 2010; Jones and Rebelo, 2013; Razgour et al., 2013; Sherwin et al., 2013; Ancillotto et al., 2016). Bats may also exhibit a behavioural shift throughout the winter, with foraging flights more frequent due to the increasing availability of food sources in winter warm conditions (Stepanian and Wainwright, 2018). These behavioural changes can be drivers of bat population dynamics (Reusch et al., 2019), as warmer temperatures can influence both bat physiological responses and the development and availability of insect communities (Roitberg and Mangel, 2016).

Climate change is expected to impact severely the European fauna (particularly in southern Europe) in the near future, with significant potential losses in its diversity (Araújo et al., 2011) that will not be offset by species shifts, thus producing a gradual continental biological homogenization (Ancillotto et al., 2016). An ongoing shift in bat's phenology is not only apparent in migration (Stepanian and Wainwright, 2018), as particular weather conditions at different seasons may result

in species-specific responses, depending on their respective foraging strategy and hibernation phenology (Reusch et al., 2019), thus affecting the circadian pattern to arousals through winter. However, studies on the potential climate change impacts, bat adaptation and/or behaviour adjustments, especially in winter, are scarce (Sherwin et al., 2013).

To test this hypothesis, we collected data to quantify the winter nocturnal activity of a community of bats from a valley in Northern Portugal, in which nearby NSBHS and SHBS winter roosts are known, with characteristic Mediterranean-type climate conditions, in order: (1) to determine which meteorological variables had a significant influence on NSHBS and SHBS presence and activity patterns; (2) to understand how instantaneous and cumulative (last 48 hours) weather conditions influenced NSHBS and SHBS activity patterns.

Material and methods

Study area

The study area is located in the lower Sabor river valley, northern Portugal (41°21′ N, 7°5′ W) (Fig. 1), encompassing the municipalities of Torre de Moncorvo and Alfândega da Fé. The Sabor river valley altimetry varies between 130 m and 1150 m a.s.l. and it is located in the transition between the Mediterranean and Euro-Atlantic biogeographic regions, where the climate is characterized by warm summers (average temperature of 24.0 °C) and relatively mild winters (average temperature of 7.8 °C) with an average annual temperature of approximately 12.7 °C (www.ipma.pt). Precipitation follows a typical Mediterranean regime, with a clear maximum in autumn/winter (rainy season) and scarce precipitation in spring and summer (dry season), occasionally associated with heavy precipitation events and thunderstorms. The study area is surrounded by a rugged mountain matrix, with deep valleys and steep rocky slopes. These orographic and climatic features heavily reflect on the overall landscape and ecosystems of the study area: sparse areas of perennial oaks (*Quercus suber*; *Q. ilex*) and juniper (*Juniperus oxycedrus*) forests and native shrubland, interrupted by almond and olive orchards mixed with extensive agriculture patches. The main terrestrial ecosystem interface with the Sabor river is represented by riparian vegetation that follows the majority of its course.

Bat acoustic monitoring

Data on winter bat activity was collected daily at two sampling sites (Fig. 1) and throughout two entire main bat hibernation periods (from November to February) (Dietz et al., 2009), thus totalizing eight months from 2017–2018 and 2018–2019. The two sampling points were in the same type of habitat. The upstream sampling site is located about 10 km from the river mouth, at an elevation of 170 m, whereas the downstream sampling site is located about 3 km from the river mouth, at an elevation of 150 m. The distance between the two sampling sites is of approximately 7 km, thus avoiding pseudoreplication. These two sampling sites were chosen due to the following experimental requirements: (1) the previous confirmation of winter bat activity indicia; (2) the nearby presence of an automatic weather station; and (3) the known location of surrounding roosts for both groups of species (NSHBS and SHBS).

During this period, bat acoustic monitoring was carried out by using automatic passive ultrasound detectors. In order to cover a common period compatible with the emergence of most bat species, a continuous sampling detection was applied during each recording session, starting 30 minutes after sunset and ending three hours later. The detectors were securely attached to a wooden pole and placed at approximately 4 meters above the ground.

The sampling metrics in the analysis comprise the number of bat passes and species richness recorded by hourly (hour 1, hour 2 and hour 3) sub-samples (Miller, 2001; Russo et al., 2019). Bat passes were defined as a minimum of two bat echolocation calls with at least 2 ms of duration (Weller and Baldwin, 2012). The daily activity frequency (a proxy of bat arousals) was obtained by dividing the total number of sampling days by the number of days that a particular bat species was active.

Two full spectrum SM4 recorders with SMM-U1 omnidirectional ultrasonic microphones (Song Meter SM4BAT FS; Wildlife Acoustics Inc., Massachusetts, USA) were used simultaneously, one in each sampling site. The units were powered with internal batteries (1.5 V, D-cell, alkaline) that were replaced every two months. Recordings were stored on high performance Secure Digital cards (SDXC with 256 GB storage space) in uncompressed wave format. The detector was calibrated to be automatically triggered by all bat vocalizations, including the low-frequency calls of some species. Therefore, a 12 dB gain setting without 16 kHz high filter was used to boost the audio signal input level coming from the microphone to ensure that low amplitude signals were detected. The sampling rate was 256 kHz and the minimum duration of a signal was defined as 1.5 ms. For recording lower-frequency species (e.g. *Tadarida teniotis*) the minimum trigger was defined at 10 kHz and the digital trigger level at 12 dB. A recording trigger window setting was selected at 3 s, with a 15 s maximum length.

Echolocation analysis

We used a two-step process to identify call sequences. Firstly, Kaleidoscope Pro (version 4.5.5) software (Wildlife Acoustics Inc., USA) was used to automatically identify call sequences, using the intermediate setting for balanced sensitivity. The settings used for signal parameters were: signal of interest (8–180 kHz, 2–500 ms, minimum 2 calls), classifiers (bats of Europe 4.3.0, sub-region Portugal). Secondly, all bat identifications were manually verified based on seven parameters that were estimated using the screen cursors and the oscillogram: initial; medium and final frequency; maximum energy frequency; bandwidth; duration and inter-pulse interval. Species identification (including social calls), genus or complex phonic groups were processed by comparing the parameters of each variable with the Portuguese bat vocalization identification key (Rainho et al., 2011), other specialized bibliography (Pfalzer and Kusch, 2003; Siemers et al., 2005; Davidson-Watts et al., 2006; Walters et al., 2012; Barataud et al., 2015; Horta et al., 2015), as well as our own calls library. We also quantified bat foraging activity by counting the number of feeding buzzes (i.e., bat final approach towards prey, distinguishable by the emitted call structure) present within a bat pass.

In the case of species with overlapping echolocation parameters, the calls were matched to possible pairs or groups of species (e.g., *Eptesicus* spp./*Nyctalus* spp., *Eptesicus* spp./*Nyctalus leisleri*, *Miniopterus schreibersii*/*Pipistrellus pygmaeus*, *Myotis blythii*/*M. myotis*, *Nyctalus lasiopterus*/*N. noctula*, *Pipistrellus kuhlii*/*P. pipistrellus* and *Pipistrellus pipistrellus*/*P. pygmaeus*). However, in the particular case of *Pipistrellus* genus: *P. kuhlii*, *P. pipistrellus* and *P. pygmaeus*, the records could be clearly distinguished by their respective social call analysis. All vocalizations that could not be undoubtedly assigned to a given species/genus/phonic group were classified as unidentified records.

Meteorological variables

Bat activity is influenced by weather conditions (Ciechanowski et al., 2007) and, hence, we included several meteorological variables to assess their potential effects. The meteorological variables (precipitation

– PREC; temperature – TEM; relative humidity – HUM; wind speed – WS and wind direction – WD) (Supplementary material S1) were recorded hourly, and simultaneously with the bat acoustic monitoring, by a site automatic weather station (AWS) (temperature and humidity sensor – model HMP45A, Vaisala, Helsinki, Finland; wind direction and wind speed sensor – model WINDSONIC, Gill, Hampshire, UK; precipitation sensor – model 52203, Young, Michigan, USA). The AWS is located in between the two bat acoustic sampling sites, which are at a distance of approximately 3.5 km from each other (Fig. 1). Bat arousal episodes can simply reflect the persistence of an endogenous circadian trigger for activity. Having this in mind, we recorded the cumulative (last 48 hours) weather conditions (cumulative precipitation – PREC_48, average temperature – TEM_48, average relative humidity – HUM_48, average wind speed – WS_48 and average wind direction – WD_48) over the last 48 hours before surveys (Supplementary material S1). In most studies on bat activity, the weather variables are usually monitored in the last 24 hours of the warm seasons. However, we consider that for the winter period the analysis of weather variables should be extended further. The last 48 hours before surveys seemed to be a good trade-off between bat metabolic (Dunbar and Brigham, 2010) and insect responses. A preceding period of weather conditions longer than 24 hours may enable capturing more representative cause-effect relationships for torpor breaks of hibernating bats (Hayes, 1997; Turbill, 2008; Johnson et al., 2012; Barros et al., 2017). Wind direction was categorized by quadrants, where each quadrant was centered on the four cardinal directions (North, East, South and West).

Statistical analysis

To compare the activity patterns of SHBS and NSHBS throughout the different months, a nonparametric Kruskal-Wallis test was used to examine differences between activity (number of bat passes) among months complemented by the Tukey and Kramer (Nemenyi) post hoc pairwise comparisons test to determine the differences between months using the package `PMCMR` (Pohlert and Pohlert, 2016).

The Generalized Linear Mixed Models (GLMM) were run considering all (valid) combinations of explanatory variables for the winter bat activity, using the R package `lme4` (Bates et al., 2015). In order to avoid high multicollinearity, the explanatory variables were selected after a pairwise correlation analysis using Spearman's rho correlation coefficient and only predictors with correlation lower than 0.7 (Dormann et al., 2007) and Generalized Variance Inflation Factor lower than 5 (Chatterjee et al., 2006) were considered by using the `corvif` function, R package `AED` (Zuur et al., 2010).

The bat activity (bat passes) was grouped by the response variables: (i) NSHBS; (ii) SHBS. The meteorological variables are assumed as explanatory variables (fixed effects). According to the features of the response variable (bat passes) and potential overdispersion, we performed GLMMs with Poisson error distribution and a negative binomial distribution (`link=log`) for each response variable (Zuur et al., 2009). However, since the models did not fit (by examination of residual plots) (Breheny and Burchett, 2013), we transformed the continuous response variable into a discrete one (i.e., with and without bat
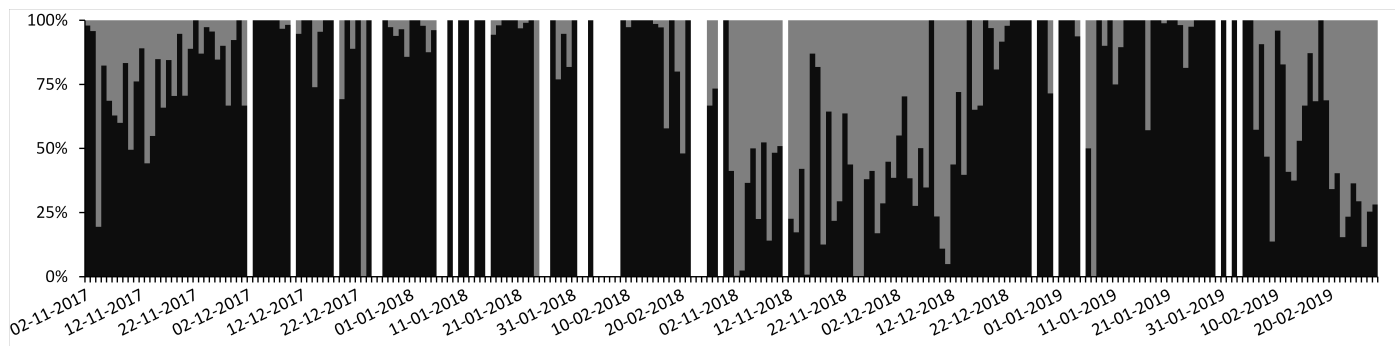

Figure 2 – Relative passes of non-strictly hibernating bat species (NSHBS - black bars) and strictly hibernating bat species (SHBS - grey bars) per night throughout the study period.
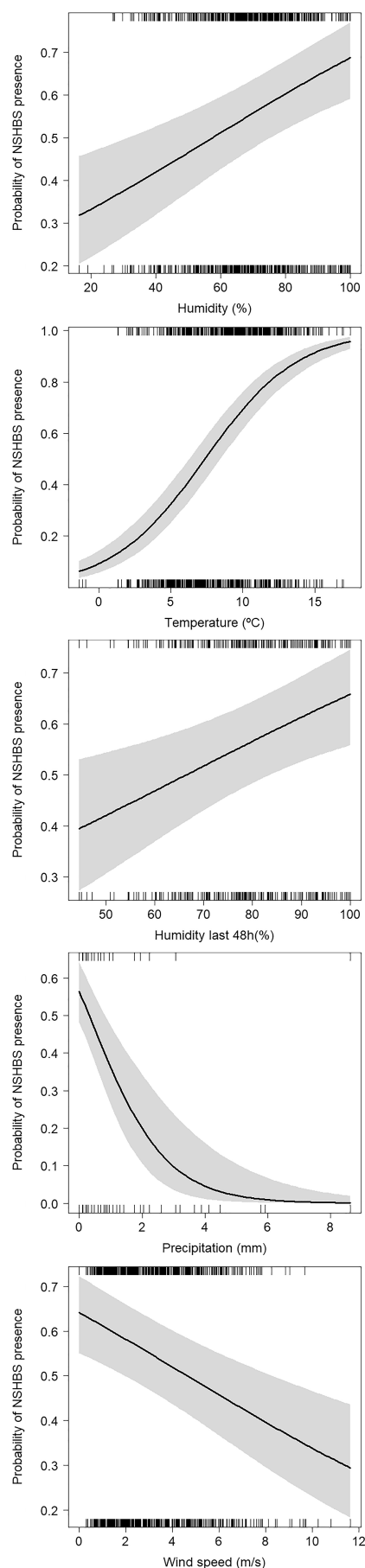
Figure 3 – Estimated relationships between NSHBS probabilities and significant variables (HUM, PREC, TEM, WS and HUM_48) in NSHBS best model. The light grey ribbon represents the 95% confidence interval, and the solid black lines indicate the estimated values. Black tick marks represent raw data values.

passes), as a presence/absence variable with a binomial error distribution (`link=logit`) for the respective analysis (Zuur et al., 2009). This was carried out to quantify the potential influence of the explanatory variables (weather conditions) in each response variable (Supplementary material S1). According to our sampling hierarchical structure design (i.e., simultaneous recordings of bat activity at two sampling sites on the same night), we treated site and hours (Supplementary material S1) as random effects (Zuur et al., 2009). We included hours and site as parameters in the models, as a random effect, to identify possible inter-night and inter-site variations. To outline a general pattern and obtain robust models, data from the two sampling sites were analysed as a single dataset.

We generated, based on full models, a set of candidate models containing all possible variable combinations ranked by the corrected Akaike Information Criterion (AIC), using the dredge function package `MuMIn` (Barton, 2017). We selected the best model based on the AIC performance metric (Burnham and Anderson, 2002). Plots of residuals were examined to check the assessment, appropriateness and validation of the fitted models (Breheny and Burchett, 2013) (Supplementary material S2). All statistical analyses were performed using R v3.3.3 software (R Core Team, 2017), using the `Rcmdr` package (Fox, 2005; Fox and Bouchet-Valat, 2006; Fox, 2016) and the R packages `PMCMR` (Pohlert and Pohlert, 2016) `lme4` (Bates, 2007), `MASS` (Venables and Ripley, 2002), `blmeco` (Korner-Nievergelt et al., 2015), `MuMIn` (Barton and Barton, 2013), `AED` (Zuur et al., 2010), `visreg` (Breheny and Burchett, 2013) and `DHARMa` (Hartig, 2017).

Results

Winter bat activity patterns

During the two monitored hibernation periods, in a total of 239 acoustic recording sessions, we obtained 1434 hours of bat pass recordings, distributed equitably by the two sampling sites. Overall, we recorded 21997 bat passes during the study period, with temperatures that varied between −1.3 °C and 17.0 °C, with an average of 6.7 °C (SD ±3.2 °C). From the survey analysis, 12 species and 4 genera were identified, complemented by 8 additional pairs or species groups, in which was not possible to confidently distinguish the species through acoustic analysis, or when there are species with overlapping echolocation parameters, totalizing a bat richness of eighteen potential species (Tab. 1). The most commonly recorded species was *T. teniotis* (n=12337 passes), followed by *P. pipistrellus/P. pygmaeus/M. schreibersii* group (n= 4090); *P. pygmaeus/M. schreibersii* (n=2860); *P. kuhlii* (n=1334); *P. pipistrellus* (n=872) and *P. pygmaeus* (n=254). The records of *T. teniotis* represented 56.1% of the total dataset combining species, pairs and groups (Tab. 1 and Fig. 2). The longest period without any activity at the sampling sites was of five days (between 4 February 2018 and 8 February 2018) (Fig. 2). During the study period, the activity frequency (a proxy of bat arousals) for the most common species/groups was, on average, 1.2 days for *T. teniotis*, 4.7 days for *P. kuhlii*. 3.0 days for *P. pipistrellus*, 6.2 days for *P. pygmaeus*, 2.5 days for *P. pipistrellus/P. pygmaeus/M. schreibersii* and 2.2 days for *P. pygmaeus/M. schreibersii* (Tab. 1). On average, bats were detected in 81.6%, 57.7%, 48.3% and 55.9% of the nights sampled in November, December, January and February, respectively.

The activity patterns of the NSHBS differed among months (Kruskal-Wallis test: $\chi^2= 4.08$, df=3, $p<0.001$) with significantly highest number of bat passes detected in November. In the same way, the Kruskal-Wallis and the Nemenyi tests confirmed the significant differences between months in the bat passes of the SHBS (χ^2=272.76, df=3, $p<0.001$), with activity levels significantly higher in November and lower in January when compared with the records obtained in the other months.

A total of 251 acoustic records were identified with feeding buzzes (1.1% of total bat passes), the species that exhibited foraging activity were *P. pygmaeus* (32.9%), *T. teniotis* (22.0%), *P. kuhlii* (17.5%), *P. pipistrellus* (10.9%), *P. pygmaeus/M. schreibersii* (7.0%), *M. schreibersii* (5.0%), *P. pipistrellus/P. pygmaeus/M. schreibersii* (3.7%), *P. pipistrellus/P. pygmaeus* (0.7%) and *B. barbastellus* (0.1%). The month

Table 1 – Number of bat passes (BP), species richness, number of feeding buzzes and social calls recorded during the study period. Mean and standard deviation (SD) of bat passes per hour, expressed by month. Relative bat passes (%) detected and frequency of activity in days for the entire study period are also listed.

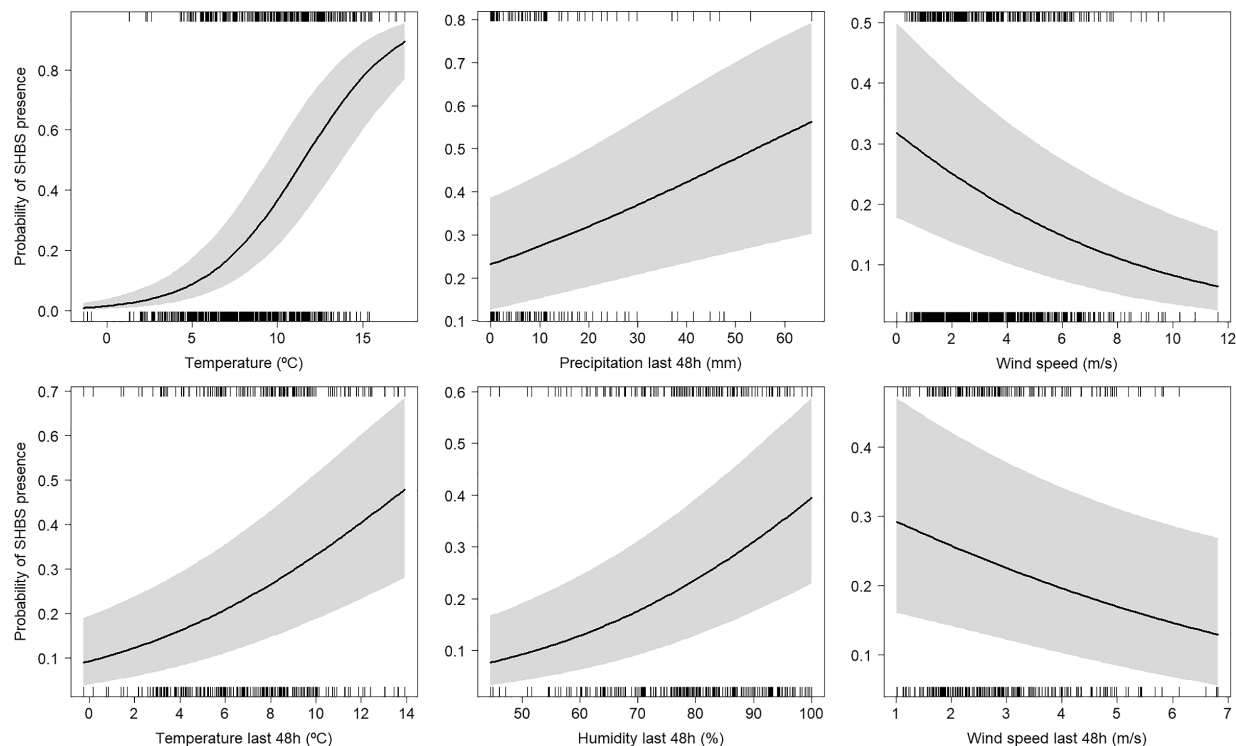| Year	2017				2018								2019				Relative bat Passes %	Activity frequency (days)
Month	November		December		January		February		November		December		January		February			
Species/Sp. Group	BP	Mean±SD	BP	Mean±SD	BP	Mean±SD	BP	Mean±SD	BP	Mean±SD	BP	Mean±SD	BP	Mean±SD	BP	Mean±SD		
Tadarida teniotis	1588	9.12 ±18.40	878	4.72 ±4.70	617	3.370±6.739	893	5.31 ±16.50	4996	27.75 ±65.50	1946	10.46 ±29.00	585	3.14 ±7.00	834	4.96 ±9.20	56.10	1.2
Pipistrellus kuhlii	50	0.28 ±1.40	10	0.05 ±0.10	1	0.01 ±0.10	9	0.05 ±0.30	1049	5.82 ±21.60	161	0.86 ±8.00	0		54	0.32 ±1.80	6.10	4.7
Pipistrellus pipistrellus	71	0.40 ±1.10	4	0.02 ±0.10	4	0.02 ±0.10	30	0.17 ±1.80	198	1.1 ±2.7	79	0.42 ±1.60	6	0.03 ±0.20	486	2.89 ±12.00	4.00	3.0
Pipistrellus pygmaeus	12	0.06 ±0.40	0		0		0		140	0.77 ±2.20	11	0.05 ±0.40	0		91	0.54 ±2.00	1.20	6.2
Miniopterus schreibersii	1	0.01 ±0.10	2	0.01 ±0.10	1	0.01 ±0.10	0		48	0.26 ±0.80	16	0.08 ±0.30	0		6	0.03 ±0.10	0.30	6.9
Myotis daubentonii	4	0.02 ±0.10	0		0		1	0.01 ±0.10	14	0.07 ±0.30	0		0		2	0.01 ±0.10	0.10	13.4
Hypsugo savii	3	0.01 ±0.10	1	0.01 ±0.10	0		2	0.01 ±0.10	10	0.05 ±0.30	0		0		0		0.10	24.1
Nyctalus leisleri	2	0.01 ±0.10	8	0.04 ±0.10	1	0.01 ±0.10	0		3	0.01 ±0.10	0		2	0.01 ±0.10	0		0.10	30.1
Myotis escalerai	1	0.01 ±0.10	0		0		0		2	0.01 ±0.10	1	0.01 ±0.10	0		0		0.01	60.3
Barbastella barbastellus	0		1	0.01 ±0.10	0		0		2	0.01 ±0.10	1	0.01 ±0.10	0		1	0.01 ±0.10	0.01	48.2
Rhinolophus ferrumequinum	0		1	0.01 ±0.10	2	0.01 ±0.10	1	0.01 ±0.10	1	0.01 ±0.10	0		0		1	0.01 ±0.10	0.01	40.2
Rhinolophus euryale	0		0		0		0		1	0.01 ±0.10	0		0		0		0.01	241.0
Eptesicus sp.	0		0		0		0		1	0.01 ±0.10	0		4	0.02 ±0.10	1	0.01 ±0.10	0.01	48.2
Nyctalus sp.	0		0		0		0		6	0.03 ±0.20	2	0.01 ±0.10	0		0		0.01	60.3
Plecotus sp.	4	0.02 ±0.10	2	0.01 ±0.10	1	0.01 ±0.10	0		7	0.03 ±0.20	2	0.01 ±0.10	2	0.01 ±0.10	11	0.065±0.300	0.10	11.5
Myotis sp.	3	0.01 ±0.10	0		0		2	0.01 ±0.10	6	0.03 ±0.20	0		0		0		0.10	24.1
P. pipistrellus/P. pygmaeus/M. schreibersii	33	0.18 ±0.50	3	0.01 ±0.10	2	0.01 ±0.10	0		2479	13.77 ±24.10	780	4.19 ±10.60	21	0.11 ±0.90	772	4.59 ±12.00	18.60	2.5
P. pygmaeus/M. schreibersii	134	0.77 ±1.30	3	0.01 ±0.10	9	0.04 ±0.20	14	0.08 ±0.30	1658	9.21 ±17.30	770	4.13 ±9.50	4	0.02 ±0.10	268	1.59 ±5.10	13.00	2.2
P. pipistrellus/P. pygmaeus	14	0.08 ±0.20	3	0.01 ±0.10	0		0		10	0.05 ±0.20	2	0.01 ±0.10	0		0		0.10	11.0
Myotis myotis/Myotis blythii	0		1	0.01 ±0.10	0		0		2	0.01 ±0.10	0		0		0		0.01	80.3
Myotis emarginatus/M. bechsteinii	0		1	0.01 ±0.10	0		1	0.005±0.100	3	0.01 ±0.10	0		0		4	0.023±0.100	0.01	26.8
Nyctalus lasiopterus/Nyctalus noctula	0		1	0.01 ±0.10	0		0		1	0.01 ±0.10	0		0		0		0.01	120.5
Rhinolophus mehelyi/R. euryale	0		0		0		0		0		0		0		1	0.005±0.100	0.01	241.0
Eptesicus sp./N. leisleri	0		1	0.01 ±0.10	0		1	0.005±0.100	1	0.01 ±0.10	0		0		0		0.01	80.3
Richness	10		12		7		9		17		12		6		12			
Foraging activity (feeding buzzes)	54		2		0		5		101		31		2		56			3.9
Socialization activity (social calls)	19		23		18		24		715		101		0		360			3.3

Figure 4 – Estimated relationships between SHBS probabilities and significant variables (TEM, WS, HUM_48, PREC_48, TEM_48 and WS_48) in SHBS best model. The light grey ribbon represents the 95% confidence interval and the solid black line indicates the estimated values. Black tick marks represent raw data values.

with most foraging activity was November 2018. Only one month (January 2018) did not exhibit any record of feeding buzzes (Tab. 1). A total of 1260 acoustic records were identified as social calls (5.4% of total bat passes), of which the species/groups with the highest social activity were *P. pygmaeus* (29.4%), *T. teniotis* (22.0%), *P. pipistrellus* (16.9%), *P. pygmaeus/M. schreibersii* (15.0%), *M. schreibersii* (9.8%), *P. pipistrellus/P. pygmaeus/M. schreibersii* (5.6%) and *P. kuhlii* (1.0%). The month with the highest social activity was November 2018. In contrast, January 2019 remained without any record of social interactions (Tab. 1). Along the study period, we recorded, on average, feeding buzzes every 3.9 days and social calls every 3.3 days. The lowest temperature at which foraging (*Tadarida teniotis*) and social activity (*Pipistrellus pipistrellus*) were observed was 4.5 °C and 2.6 °C, respectively.

Overall, November 2018 displayed the highest global bat activity (bat passes, feeding buzzes and social calls) for the most common species/group, namely *T. teniotis*, *P. pipistrellus/P. pygmaeus/M. schreibersii*, *P. pygmaeus/M. schreibersii* and *P. kuhlii*, also being the month with the highest foraging (feeding buzzes, n=101) and social activity (social calls, n=715) (Tab. 1).

The influence of weather conditions on winter bat activity

The a priori correlations among the explanatory variables revealed no significant multicollinearity, enabling the subsequent analysis of the candidate models. We then performed a GLMM selection procedure for the full NSHBS dataset and in the five models that showed the best performance (ΔAIC<2). As the variables HUM, PREC, TEM, WS and HUM_48 were retained by all models, they were thereby incorporated in the best NSHBS model (Tab. 2). Regarding the full SHBS models selection, in the four models that performed the best (ΔAIC<2), the variables TEM, WS, HUM_48, PREC_48, TEM_48 and WS_48 were retained in all of them and subsequently included in the best SHBS model (Tab. 2).

Our analysis demonstrated that instantaneous and cumulative weather conditions had different impacts on NSHBS and SHBS (Tab. 3, Fig. 3 and Fig. 4). We observed a significant positive effect of TEM, HUM and HUM_48 and significant negative effect of PREC and WS in the presence of NSHBS (Tab. 3 and Fig. 3). The presence of SHBS was positively influenced by the TEM, TEM_48, HUM_48 and PREC_48

and negatively by WS and WS_48 (Tab. 3 3 and Fig. 4). All the cumulative variables in the best model, i.e., considering the preceding meteorological conditions, reveal statistically significant cause-effect relationships with the presence of SHBS (Tab. 3). On the other hand, the presence of NSHBS is only influenced by the 48-hour humidity (Tab. 3). Generally, higher temperature, humidity and lower wind speed (prevailing during the preceding 48 hours) were associated with the presence of NSHBS and SHBS (Fig. 3, Fig. 4). Although the presence of NSHBS (Fig. 3) decreases with precipitation, the presence of SHBS increases with the last 48-hour cumulative precipitation (Fig. 4).

Regarding the NSHBS best model fitness tests, 23.4% of variances were explained by fixed predictors (R2m in Tab. 3), and only 1.6% of variances were explained by random predictors (R2m – R2c in Tab. 3). In the SHBS best model, 35.8% of variances were explained by fixed predictors (R2m in Tab. 3), and 5.5% of variances were attributed to fixed and random predictors (R2m – R2c in Tab. 3). Overall, these results confirm a high proportion of variance explained by the fixed predictors to the variations in the presence of NSHBS and SHBS, compared with the low proportion of variance explained by the random predictors (Tab. 3).

Discussion and Conclusions

Bat winter activity has been previously reported in other studies, mostly by monitoring bat activity in hibernacula, inside roost or at their entrance (Bartonička and Řehák, 2004; Schwab and Mabee, 2014; Vlaschenko and Naglov, 2018), guano samples analysis (Miková et al., 2013; Hope et al., 2014), radio-telemetry (Johnson et al., 2012) or bat captive experiments (Hays et al., 1992). Only a few of them include activity rates obtained from continuous field acoustic monitoring in foraging habitats (White et al., 2014; Zahn and Kriner, 2016; Barros et al., 2017), but none with a daily temporal resolution throughout all the bat hibernation period. In this context, our study provides unique information on daily winter bat activity patterns, outside hibernacula in a Mediterranean region.

Our work demonstrates that bat winter activity in this Mediterranean region can occur with temperatures between −1.3 °C and 17.0 °C, although mostly concentrated in nights with temperatures above the seasonal mean (6.7 °C ± 3.2 °C). A similar pattern of bat activity was

Table 2 – Most parsimonious and best models of multi-model inference ranked by ΔAIC<2, used to test the influence of meteorological variables in NSHBS and SHBS presence, during winter in the study area. Te top best model is indicated in bold. It shows the number of estimated parameters (K), Akaike Information Criterion (AIC), the difference in AIC score (ΔAIC) compared to the model with the lowest AIC score, model weights (wi).

Model number	Intercept	HUM	PREC	TEM	WD	WS	HUM_48	PREC_48	TEM_48	WD_48	WS_48	K	AIC	ΔAIC	wi
NSHBS															
372	**-4.673**	**0.019**	**-0.822**	**0.305**		**-0.126**	**0.016**					**9**	**1726.8**	**0.00**	**0.130**
380	-4.510	0.018	-0.823	0.304		-0.134	0.016	0.011		-0.067		10	1727.8	1.07	0.076
884	-4.884	0.018	-0.839	0.307		-0.133	0.018	0.010			0.045	10	1728.0	1.27	0.069
376	-4.585	0.018	-0.824	0.030	-0.018	-0.128	0.016	0.012				10	1728.7	1.92	0.050
852	-5.134	0.018	-0.850	0.312		-0.136	0.021				0.073	9	1728.7	1.95	0.049
SHBS															
1011	**-7.327**			**0.3547**		**0.157**	**0.037**	**0.021**	**0.162**		**-0.161**	**10**	**1375.7**	**0.00**	**0.185**
1012	-7.291	-0.006	-0.255	0.3442		-0.152	0.043	0.020	0.169		-0.158	11	1376.3	0.64	0.134
1015	-7.662		-0.274	0.3618	0.071	-0.148	0.039	0.021	0.159		-0.153	11	1376.4	0.78	0.125
1016	-7.557	-0.005	-0.253	0.3517	0.055	-0.146	0.043	0.020	0.166		-0.152	12	1377.7	1.99	0.068

observed in other studies (White et al., 2014; Zahn and Kriner, 2016; Barros et al., 2017). According to our results, bat activity is a relatively common phenomenon in winter, with a monthly variation from 48.3% to 81.6% of the nights. Although the activity pattern is similar to other studies with lower activity in January, the rate of activity days in our study was higher than other studies have shown. In southeastern Nebraska, North America, the activity rate was between 27.0% and 67.0% of the nights (White et al., 2014), and in Bavaria, southern Germany, between 14.3% and 82.6% of the nights (Zahn and Kriner, 2016). Most of these differences in winter activity may be explained by dissimilarities in the thermal characteristics of the roosts, different composition of species diversity and lengths of the hibernation period (Rodrigues, 2003). In fact, winters in some regions of North America or Germany are characterized by severer conditions, with heavy snowfall and temperatures far below zero, not comparable to those of our study area, marked predominantly by a Mediterranean climate with relatively mild winters.

Our study demonstrates that the bat winter activity in this Mediterranean region can occur in all winter months. The high bat activity of NSHBS and SHBS in November was expected, since it is the beginning of winter, when the usual persistence of favourable weather conditions may determine bat hibernation delays or more torpor breaks (White

et al., 2014). However, in contrast with the lower activity patterns of the SHBS in January, due to the thermal behaviour of the NSHBS (*Tadarida teniotis*), characterized by short periods of torpor including under adverse weather conditions (Ibáñez and Pérez-Jordá, 1998; Arlettaz et al., 2000), the activity level of the NSHBS in January was frequent.

Seasonal activity through acoustic and visual observations has shown spatial mobility of *Tadarida teniotis* (NSHBS) in Switzerland and Spain in winter (Arlettaz et al., 2000; Balmori, 2003) and is geographically restricted by the availability of warm roosts during the winter season (Arlettaz et al., 2000). This high arousal frequency in winter seems to result from a higher metabolic rate imposed by the selection of warm roosts and more rapid depletion of fat reserves (Arlettaz et al., 2000; Balmori, 2018). The frequency of arousals of *Tadarida teniotis* (NSHBS) in winter appeared quite high when compared to the other families (Vespertilionidae and Rhinolophidae) (SHBS) also present in our study area, mainly under adverse weather conditions. A similar pattern was also described in Arlettaz et al. (2000).

The high activity and the foraging pattern activity obtained reveal that these are not simply sporadic bouts, but repeated high activity events or perhaps even a continuous activity pattern. As expected, *T. teniotis* (NSHBS) shows shorter torpor bouts duration due to their thermal behaviour (Arlettaz et al., 2000) and feeding needs. For the rest of the species (SHBS), the causes of winter activity and foraging behaviour are unknown. They can be either a response to immediate nourishment needs (due to unfavourable roost conditions) or an opportunistic behaviour of some individuals to add up some additional caloric intake (Zahn and Kriner, 2016). In our study, the activity frequency (a proxy of arousals) of *T. teniotis* in winter appeared quite high. For instance, we observed an average frequency of 1.2 days between records, a rate somewhat higher than verified in other studies (Arlettaz et al., 2000), where *T. teniotis* activity frequency was of 3.4 days on average. Although these differences may be explained by the winter prevailing conditions in different regions, with concomitant distinct thermal requirements, the local context, namely in terms of roosts quantity and proximity, can also play an important role in these activity patterns (Hayes et al., 2009). For other more common species (*Pipistrellus* sp.), the activity frequency varied between 2.2 and 6.9 days. Therefore, these wintering behaviour patterns, particularly the activity frequency of SHBS, are of major relevance given the expected change of winter temperature patterns driven by climate change.

Table 3 – Best GLMM model results using an information-theoretic approach based on Akaike's Information Criterion (AIC) on NSHBS and SHBS presence, during winter in the study area. Estimates, standard error (SE) and standard deviation (SD), Z-values and associated *p*-values expressed with a log link due to the binomial distribution used in GLMM. Standard error (SE) for fixed effects and standard deviation (SD) for random effects. Marginal R^2 (R^2m) Conditional R^2 (R^2c).

Response variable	Predictor variable	Estimate	SE/SD	Z value	*p*-value
NSHBS	Intercept	-4.829	0.558	-8.655	<0.001
	TEM	0.309	0.023	13.200	<0.001
Fixed effects (R^2m=0.234)	HUM	0.018	0.004	4.043	<0.001
	PREC	-0.824	0.174	-4.722	<0.001
	WS	-0.125	0.031	-4.022	<0.001
	HUM_48	0.019	0.006	3.006	0.002
Random effects ($R^2c − R^2m$=0.016)	HOUR		0.268		
	SITE		0.023		
SHBS	Intercept	-7.238	0.825	-8.769	<0.001
	TEM	0.357	0.032	10.855	<0.001
	WS	-0.163	0.037	-4.389	<0.001
Fixed effects (R^2m=0.358)	TEM_48	0.157	0.032	4.867	<0.001
	HUM_48	0.037	0.006	5.399	<0.001
	PREC_48	0.022	0.006	3.262	0.002
	WS_48	-0.176	0.065	-2.678	0.007
Random effects ($R^2c − R^2m$=0.054)	HOUR		0.323		
	SITE		0.444		

The feeding buzzes were recorded in a high number of species and this behaviour was exhibited in almost all months (except in January 2018), thus suggesting frequent foraging attempts. In fact, our study has a foraging rate of 1.1% of total bat passes. Unfortunately, the rates of this behaviour for winter bat activity are not described in the available literature since systematic studies with this approach are scarce (Klüg-Baerwald et al., 2016; Zahn and Kriner, 2016; Barros et al., 2017). The results of our study demonstrate a significant level of social

behaviour (5.4% of total bat passes). Due to the high activity recorded it was expected that this behaviour pattern, is likely used to guide the displacement between roosts maintaining the social cohesion of colonies (Sedgeley, 2001). In fact, in nights of great winter activity bats exhibit social behaviours (Parsons et al., 2003). Therefore, it is not known whether and how frequent are winter foraging and social behaviour, which makes this approach a challenge for future studies on the impacts of warmer conditions under climate change.

Among other multi-factorial environmental drivers, weather conditions can play a major role by determining bat activity patterns (Hays et al., 1992; Turbill, 2008; Johnson et al., 2012; Barros et al., 2017). Bat winter activity seems to occur primarily on occasional nights of mild weather conditions (Turbill, 2008). With extreme weather events estimated to increase in frequency and a decrease in cold weather-related indices (e.g., decrease of frost days or days with minimum temperatures below 0 °C), the levels of activity of many bat species living in temperate regions are expected to considerably increase (Park et al., 2000). Thus, weather conditions can play an important role in determining bat activity patterns and the understanding of how winter weather factors influence global bat activity. For some species, in particular, this is critical and a major goal for bat conservation. This is especially true when it comes to understanding the consequences brought by climate change on bat activity and all consequences on their conservation guidelines and measures. These are, for instance, possible shifts on bat distribution range or the anticipation of the breeding season beginning, as already recorded for *Myotis myotis* in Portugal (Luísa Rodrigues, *pers. comm.*, 2020). Our results clearly demonstrate that instantaneous and cumulative weather conditions produce different effects on NSHBS and SHBS winter activity, with a clear trend towards the importance of cumulative weather conditions for SHBS. In fact, the SHBS group is positively influenced by the precipitation in the last 48 hours. These activity patterns can be explained by the fact that winter raining nights tend to be slightly warmer in the Mediterranean areas, increasing the potential availability of insect communities and the opportunities for energy intake and/or for middle winter roost changes. In other words, SHBS require previous events of longer favourable weather conditions to become active. Something that NSHBS do not need, as they are more dependent on instantaneous weather conditions. The predicted climate change scenarios, leading to a higher frequency, intensity and duration of extreme weather and climate events, including warm winter spells, may have a significant influence on the hibernation ecology of SHBS, increasing the winter activity frequency and/or replacements to cooler roosts.

Bats in Europe are expected to show a negative response to the ongoing ecological and climate changes with a redistribution tendency towards the north (Lundy et al., 2010; Rebelo et al., 2010) in the mid-to-long term, especially in the southern range of their distribution (Lundy et al., 2010; Araújo et al., 2011). This suggests that the Mediterranean might be a particularly vulnerable region for bat conservation (Rebelo et al., 2010). Furthermore, in the short-term, one other possibility that bats have is to compensate for the increased temperature in winter, changing the typical hibernacula to cooler roosts and/or more stable weather variation. In fact, most of the SHBS detected in our study are crevice dwelling bats, more exposed to airflow and fluctuating air temperatures (Wermundsen and Siivonen, 2010). Thus, winter monitoring under ongoing climate change is of major importance to fully understand the response of bats to a changing environment. This is particularly applicable to this peripheral European region, which is at the distribution limit of many bat species. Other multi-factorial environmental drivers also influence the variation of bat activity, directly or indirectly, such as food availability. Weather conditions can play an important role in determining prey availability (Meserve et al., 2016) that can affect the pattern of bouts frequency and duration of bat arousal behaviour. For future research, in addition to weather conditions, it is important to also collect information on wintering prey availability to test a more comprehensive set of driver hypothesis that may influence bat activity. Data generated from large-scale and long-term ecological

surveys can be particularly useful for isolating the weather factors that affect bats, and their relative importance.

With global climate change, the seasonal conditions are increasingly difficult to predict due to the increasing temperatures, the altered precipitation patterns, and the higher frequency of extreme weather events (IPCC, 2013). In this context, bats can act as important bioindicators of climate change because of their high sensitivity to changes in environmental conditions (Jones et al., 2009; Russo and Jones, 2015).

Climate change is expected to result in widespread population and species extinctions, and climate-related local extinctions have already been observed in hundreds of species (Urban, 2015). In this perspective, future conservation management efforts should consider local adaptation to climate change and focus not only on extinction or migration/movement of threatened bats, but also on bat behavioural and hibernation ecology. Therefore, phenotypic and behavioural plasticity should be considered key mechanisms for bats to cope with changing weather conditions under climate change scenarios (Stepanian and Wainwright, 2018). Given that conservation plans are designed based on a long-term monitoring perspective, they should consider the possibility that species-occurrence patterns may change in roosts during winter, namely due to the degradation of roost prevailing conditions for bats. So, this possible change in winter bat behavioural patterns (Jonasson and Willis, 2011; Johnson et al., 2012) is a major challenge to improve conservationist management strategies, which must be framed with scientific credibility for the global guidance of bat's conservation plans by anticipating future relevant ecological consequences associated with climate change.

Despite our current results showing a potential behavioural adaptation to climate change, it is unclear whether these potential behavioural shifts can keep up with the ever-evolving and fast-paced changing conditions. Thus, this aspect needs to be further investigated to better understand the role of possible SHBS adaptations during hibernation as a response to climate change. In conclusion, our results can improve the current knowledge on bats arousal behaviour and they are particularly suitable for management recommendations action in the scope of bats conservation programs and for decision-making, namely by anticipating future ecological consequences associated with changes of weather conditions on vulnerable bat communities in general and on Mediterranean bat species in particular. ✍

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Specification of all variables considered in this study.

Figure S2 Diagnostic plots for NSHBS best models.

Figure S3 Diagnostic plots for SHBS best models.