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Bat activity and evidence of bat migration at two high elevation passes in the Western Alps

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Abstract

Information about bat migration routes across the Alps is generally scarce and there is no existing data available for the Italian part of the chain. Through acoustic surveys, we explored the possibility that even a region characterized by high Alpine mountains may be crossed by migrant bats.

Data were recorded in August-September 2016 at two sites located near mountain passes in the Aosta Valley (NW Italy), respectively for 29 and 53 entire nights. Activity of different species/acoustic groups of species was associated with period and weather variables, the most important of which was wind speed (negatively related), followed by temperature (positively related). Only the acoustic group *N. leisleri*/*N. noctula*/*V. murinus*/*E. serotinus*, at both sites, showed a significant increase in activity in the period 31 August- 14 September. Additional elements suggesting the occurrence of a late-summer migratory flow involving this group were: the fact that it mainly consists of migratory species; the attribution to *N. leisleri* of the sequences that could be identified at the species level; the timing of activity through the night (generally later than the other bats) and some characteristics of the recorded calls.

Contacts with *B. barbastellus* were recorded at both study sites, possibly due to migrating individuals or, as an alternative, to resident bats using open environments located far from woods during the summer.

The occurrence of *P. kuhlii* was ascertained at the highest elevation so far reported for this species in the Alps (2208 m a.s.l.).

Keywords

Acoustic monitoring, Alps, bats, migration, *Nyctalus leisleri*, weather.

Introduction

Migration is a complex natural phenomenon which profoundly influences the life cycles of many species. It is a solution to avoid seasonal unfavorable conditions, but it also involves major threats: migrants are vulnerable to habitat changes that may occur along their migration routes, affecting their orientation, reducing the availability of stepping stones or exposing them to direct mortality factors (Hardesty-Moore et al. 2018). In recent years, the widespread development of wind farms has proved to be a significant threat to migratory birds and bats (e.g. Rydell et al., 2017; Thaxter et al., 2017). The importance of understanding and mitigating the impact of such infrastructures has become a goal of ecological studies, which in turn have acted as an impetus for the implementation of legislation, making it particularly important to collect accurate information on migratory routes. However, in contrast to birds, for which many detailed studies have been carried out on this topic, there is only partial information about the routes through which bats choose to migrate and the

strategies they adopt to cross or avoid ecological barriers. Some studies have suggested that they may use large rivers as landmarks for orientation and that valley bottoms are migration flyways (Strelkov 1969; Serra-Cobo et al. 2000; Furmankiewicz and Kucharska 2009). Bats have also been found to migrate along coasts (Jarzebowski 2003; Petersons 2004; Strelkov 1969) and to cross open sea (Ahlén 1997; Ahlén et al. 2007; Strelkov 1969; Walter et al. 2005; Hüppop and Hill 2016). Migrating bats can also move through mountain areas, the Alpine chain included (Bontadina et al. 2014; Widerin and Reiter 2017). In the Western Alps, migrating bat flows have been documented at Col de Jaman (1512 m a.s.l.) and at Col de Bretolet (1923 m a.s.l.), between Switzerland and France (Oppliger 2004). More recently, transits of bats, including long-distance migratory species, have been reported for a site located at 3460 m a.s.l. in the Swiss Alps, suggesting that bat migration can occur even at very high elevation (Zingg and Bontadina 2016).

At present, the routes followed by migratory bats in Italy are unknown (Hutterer et al. 2005). Here, we explored the possibility that the Aosta Valley – the northwesternmost region of Italy – may be used by migrating bats despite being characterized by mountains that are among the highest in Europe. High elevation areas are usually considered of marginal importance to bats, but their role may be overlooked: understanding if they are used by migrating bats could help to address their management more correctly, particularly considering a possible expansion of wind farming at high altitude due to the growing energy demand (although projects of this type are not currently planned at the two study sites).

Typically, data on bat migration are collected by capturing animals. This method has undoubted advantages, for example the identification of each species, but, in particular at high altitude, fixed stations with mistnets (mainly used by ornithologists to ring birds) are scarce. For this reason, we based our research on acoustic methods.

In August-September 2016, we performed acoustic surveys at two alpine passes in the Aosta Valley. Our aims were to provide a preliminary characterization of bat activity at the two sites and to verify the possible occurrence of a bat migratory flow across them. To the latter purpose we considered two aspects: I) the presence of species known to migrate, and particularly of long-distance migrants (i.e. *Pipistrellus nathusii*, *Nyctalus leisleri*, *Nyctalus noctula*, and *Vespertilio murinus*), and II) the occurrence of activity peaks that could be considered indicative of migration for being constrained to the migratory period and (compared to the activity peaks of resident species) more conditioned by the period itself than by meteorological conditions.

Materials and methods

Study area

Data were collected close to Gran San Bernardo and Piccolo San Bernardo passes.

Gran San Bernardo pass lies at an elevation of 2472 m and is the lowest pass situated along the northern boundary of Aosta Valley, which separates Italy from Switzerland. Bat activity data were recorded in the Italian territory, at about 1 km from the pass (fig. 1). The recording site, located at 45.861330° N, 7.159638° E, is identified hereafter as GSB. It coincides with “Casa don A. Carioni”, a building situated at 2208 m a.s.l. (264 m below the pass), in an open alpine landscape dominated by pastures, prairies and rocks. The site is within the SAC IT1205020, which has been designated to protect typical alpine flora and fauna species (Bocca et al. 2016).

The Piccolo San Bernardo pass has an elevation of 2188 m. It is located on the western border of Aosta Valley, between Italy and France, and is the lowest alpine pass of the northwestern Alps. Compared to the Gran San Bernardo pass, it lies further west: therefore, it is likely to be the most favorable site to cross the mountains for migrating bats engaged in NE-SW flights, i.e. in the main direction followed in Europe by long distance migratory bats (Hutterer et al. 2005). Bat activity data were recorded at 45.674900° N, 6.880534° E, inside the Chanousia Alpine botanical garden (fig. 1). The site, hereafter termed PSB, is in France, 670 m from the pass, at an elevation of 2177 m (11 m

below the pass). The small botanical garden (about 1 ha) is surrounded by alpine pastures and prairies.

Both the study areas feature harsh climatic conditions: minimum temperatures fall below zero roughly from the beginning of October to the end of May, strong winds are frequent and snowfalls particularly abundant (Mercalli et al. 2003).

Migrant birds of many species are regularly observed at the two passes, mainly during autumn migration, but no systematic study of the migration has been carried out up to now, neither at Gran San Bernardo and Piccolo San Bernardo sites nor elsewhere in the Aosta Valley. However, available data suggest that the region is crossed by minor bird migration flows (Bocca and Maffei 1997).

Surveys on the migration of noctuid moths, carried out at the Gran San Bernardo pass, proved that the area is crossed by migratory transits of these insects. While resident species are more abundant from June to the middle of August, peaks of migratory moths can occur (during periods of several nights or on single nights) both in the early and in the late summer/autumn, but they seem more important in the latter period, when flight direction is south-oriented (Hachler et al. 2002).

Data recording

Bat activity was surveyed using two Wildlife Acoustics Inc. (Maynard, MA) bat detectors: an SM2BAT+ equipped with an SMX-UT microphone at GSB and an SM4BAT FS with an SMM-U1 ultrasonic microphone at PSB. These instruments have a similar sensitivity to bat calls and it has been demonstrated that SM2 performs similarly to Batcorder 2.0 (Adams et al., 2012). Both bat detectors were positioned on the outside of isolated buildings, at about 5 m from the ground, with the microphones oriented towards each alpine pass. They were set to record automatically from about 30 minutes before sunset to sunrise, with a sampling rate of 384 kHz, trigger level 12 dB, trigger window 2 s and maximum length of recordings set to 8 s. Further settings were: Dig HPF fs/48 (8 kHz) and Dig LPF off (SM2BAT+); Min Trig Freq 10 kHz and 16k Hight Filter off (SM4BAT FS). Surveys started on 1 August 2016 and were carried out until the middle of September at GSB and until the end of September at PSB. Although the equipment was checked and the batteries replaced about every fortnight, some operating interruptions occurred, probably caused by premature exhaustion of some batteries due to low temperatures. Excluding interruptions, at GSB the survey lasted 29 nights: from 1 to 7 August (6 nights) and from 17 August to 9 September (23 nights). At PSB recording was performed continuously for 53 nights: from 1 August to 23 September.

Weather data were obtained from the nearest meteorological stations.

In the case of Gran San Bernardo, air temperature and precipitation data, measured hourly, were collected a short distance below the pass (Col Grand-Saint-Bernard, 2360 m a.s.l., weather station managed by Regione Autonoma Valle d'Aosta), at a linear distance of about 1 km from site GSB. Wind data were collected every 10 minutes at a site located about 2.3 km from GSB (Grand-Saint-Bernard Mont-Botsalet, 2500 m a.s.l., weather station managed by Regione Autonoma Valle d'Aosta); the anemometer was situated at a height of 10 m above ground level.

At Piccolo San Bernardo, all the data were collected every 30 minutes close to the pass (Col Petit-Saint-Bernard, 2188 m a.s.l., weather station managed by Osservatorio meteorologico Piccolo San Bernardo), at a distance of 900 m from PSB; the anemometer was at a height of 8 m above ground level.

Sound analysis

Sound analysis was performed in two steps.

Search-phase echolocation calls were first analyzed using the software BatSound version 4.03 (Pettersson Elektronik AB, Uppsala, S). A 512-pt Hamming window (98% overlap) was applied. We identified the echolocation sequences that could be attributed to genera or species according to the criteria presented in appendix I.

The second step of analysis was performed using the software SonoBat 3.11P (DNDesign, Arcata, CA) to measure the calls, and the identification tool iBatsID (<https://sites.google.com/site/ibatsresources/iBatsID>; Walters et al., 2012) to identify the species/acoustic groups. The procedure was applied to the sequences of echolocation calls that were not identifiable according to the criteria followed in the first step of analysis. A highly conservative approach was adopted: for each sequence several search-phase calls were examined (average 5.7) and identifications suggested by iBatsID were accepted when concordant (i.e. calls extracted from the same sequence were classified in the same way) and associated with a probability of correct classification $\geq 95\%$ for most of the calls.

In many cases, the identification procedure did not allow to definitively identify species, and was therefore interrupted at earlier stages of identification (due to groups of species with similar echolocation calls). This was the case for almost all the sequences attributed to the group composed by *N. leisleri*, *N. noctula*, *V. murinus* and *E. serotinus*. Considering the poor performance of iBatsID in the identification of *V. murinus*, we assigned the few sequences that had been attributed to this species to the same group. In some cases, we referred to an even larger species assemblage, adding to the former group a fifth species, *E. nilssonii*; this was done when some calls of the sequences were attributed to *E. nilssonii* and others to the species of the group. Finally, several sequences of poor quality QCF or FMQCF calls (not measurable by SonoBat) were attributed to *N. leisleri*/*N. noctula*/*V. murinus*/*E. serotinus* or to *N. leisleri*/*N. noctula*/*V. murinus*/*E. serotinus*/*E. nilssonii* on the basis of their shape, frequencies and bandwidth.

We did not try to identify species of the genus *Myotis*, considering both the limits of the identification tool and the scarce relevance of reaching a specific identification for bats that do not include long distance migrants. Similarly, the identification procedure was stopped at the genus level for *Plecotus* spp., since iBatsID does not consider *P. macrobullaris*, which is known to occur in the Aosta Valley.

Some echolocation sequences of poor quality, mainly represented by very faint recordings, were attributed to “chiroptera not otherwise identified”.

When present, social calls were used for specific identification, referring to descriptions reported by Russo and Jones (1999 and 2000), Pfalzer (2002 and 2007), Pfalzer and Kusch (2003), Skiba (2009), Barataud (2012) and Middleton et al. (2014).

Quantification of bat activity

Bat activity was quantified by an activity index (AI) based upon the presence/absence of defined acoustic categories during one-minute time intervals and consisting of the sum of minutes with the presence of a given category. This method was firstly proposed by Miller (2001), with reference to the species level. Compared to “bat pass” counts, it is time-saving, more objective and less inflated by the behavior of those bats that repeatedly fly within the range of the detector (a problem even more relevant if the goal of the survey is to detect transit of migrants). Furthermore, it minimizes the discrepancies that may arise from the use of different bat detectors.

However, relying on this methodological approach also poses some problems because the current methods of acoustic analysis do not allow all the acoustic sequences to be identified to the species level which can cause problems in quantifying total bat activity. When quantifying general bat activity, in order to avoid this problem, we considered the active minute with respect to the order (Chiroptera), regardless of the number of species occurring during that minute.

A second consequence of the problems encountered in call identification is that results usually comprise some categories that are not mutually exclusive (for example, in a given minute, some of the recorded sequences may be attributed to *P. kuhlii* and others to the species pair *P. kuhlii/P. nathusii*). There were therefore definitely identified calls (“certain” minutes), and those for which identification was less certain (“possibly additional” minutes). The previous example would result in one active minute for *P. kuhlii* and one “possibly additional” minute for *P. nathusii*. In these cases the analysis of data is more complicated and makes it necessary to apply one of the following solutions: pooling non-mutually exclusive categories (in the example, this means considering together the species pair *P. kuhlii/nathusii*, counting only one active minute referred to this acoustic group); examining different possibilities (case A: only one minute for *P. kuhlii*; case B: one minute for *P. kuhlii* and one for *P. nathusii*); considering only the certain case (one minute for *P. kuhlii*), while being aware of the limits this may have. We adopted the first solution (i.e. pooling data), discussing the other possibilities if relevant.

Statistical analysis

We analyzed the effect of local weather variables and period on the activity of the species/acoustic groups.

In order to select the weather data relevant to the nightly activity phase of bats, we firstly examined the acoustic recordings. Bat activity preceding sunset was never observed in the surveyed period; the earliest acoustic contact was recorded 16 minutes after sunset and the latest 37 minutes before sunrise (fig. 2). Based on these results, we selected the weather data collected between one hour after sunset and one hour before sunrise.

The local weather variables considered were total precipitation (mm), mean wind speed (m/s) and mean temperature (°C). A preliminary analysis showed a high correlation between minimum, maximum and mean temperature values, thus we selected mean temperature as representative of the entire night conditions since it was derived from multiple measurements per night.

We partitioned the data according to periods of 15 days, forming groups larger than those usually applied in the works on bird migration (5-10 days). This was decided a priori, to compensate for the relatively small sample size and to allow comparison with the few published studies which have used periods of either months or half-month periods.

In order to determine variations in species/acoustic group activity in relation to weather conditions and period, a statistical hypothesis testing framework was adopted, with the null hypothesis that bats showed a random activity in relation to weather variables and period. Univariate Generalized Linear Models (GLMs) were used. Quadratic terms for weather variables were included in the models following visual assessment of scatterplots (following Zuur et al. 2009). To reduce correlation amongst variables, we first examined all pairwise correlations to identify strongly correlated pairs ($r > |0.7|$). The result of this preliminary analysis showed that none of the above weather variables were highly collinear. To model the distribution of activity index, count (i.e. activity index values for each species/acoustic group) was initially modelled specifying a Poisson error distribution and a log link function. Since these preliminary models showed over-dispersion, a negative binomial error distribution was specified in subsequent models. The number of days of sampling per period was log-transformed and used as an offset in the model to account for the differences in the number of days sampled per period. We performed two different models, one for PSB and one for GSB, due to the difference in the sampling periods between the two sites. Data analysis was performed with R 3.5.1 (R Core Team 2018) and MASS package (Venables and Ripley 2002).

RESULTS

Taxa recorded

We identified the same taxa/acoustic groups in the two survey sites, except for the group *P. pipistrellus*/*M. schreibersii*/*P. pygmaeus*, recorded only at GSB (tab. 1).

P. pipistrellus was the species most contacted at both sites, followed by *E. nilssonii*, the group *N. leisleri*/*N. noctula*/*V. murinus*/*E. serotinus* and *H. savii* at GSB, and by the genus *Myotis* and the group *N. leisleri*/*N. noctula*/*V. murinus*/*E. serotinus* at PSB.

Among the species of the group *N. leisleri*/*N. noctula*/*V. murinus*/*E. serotinus*, only *N. leisleri* could be clearly identified. Sequences attributed univocally by iBatsID to this species, and sequences characterized by alternated call types and frequency of maximum energy of the lower calls > 22 kHz, which can be associated with high probability to *N. leisleri*, were recorded both at GSB and PSB. We never recorded alternated calls with peak frequency of the lower calls in the range 18-20 kHz, i.e. attributable to *N. noctula*.

With respect to specific identification, it must be noted that most of the echolocation sequences of this acoustic group that were recorded during the period 31 August-14 September were sequences of QCF calls, both at GSB (86% of the sequences of the group) and at PSB (73%). QCF calls are rarely used by *E. serotinus*, but they are commonly emitted by the other three species of the group.

Within the genus *Pipistrellus*, species other than *P. pipistrellus* were comparatively marginally represented in the recordings.

A social call of *P. kuhlii* was recorded at GSB on 27 August, proving with certainty the occurrence of this species at the site. Social calls of *P. nathusii* were never recorded at GSB and PSB, yet, on 14 September, we recorded an advertisement song surely emitted by this species a little below the GSB site (at Saint-Rhémy-En-Bosses, Grand Rocher hamlet, 45.823380 lat. N; 7.178397 long. E, m 1582 a.s.l.).

Several echolocation sequences were attributed to the acoustic groups *P. kuhlii*/*P. nathusii* and *P. nathusii*/*P. pipistrellus*. Some of them were sequences of QCF calls, whose identification is discussed in Appendix I. Based on the overall results of acoustic analysis (social and echolocation calls), we consider certain the presence, at least occasionally, of *P. kuhlii* both at GSB and PSB, and probable, although not confirmed with absolute certainty, the presence of *P. nathusii*.

We did not record calls certainly attributable to *P. pygmaeus*, but at GSB we recorded several sequences conservatively attributed to the group *P. pipistrellus*/*M. schreibersii*/*P. pygmaeus*. Among these, there was one sequence of QCF calls with peak energy frequency of 52.3-52.4 kHz which was recorded on 30 August and which looks likely to have been emitted by *P. pygmaeus*, since the occurrence of *M. schreibersii* at the site is considered unlikely (for the reasons discussed in Appendix I).

Some marginal activity could be attributed to genus *Plecotus* and *B. barbastellus* at both the sites. We never recorded, instead, *Tadarida teniotis*, whose loud low frequency calls are easily detectable by the instruments and the settings used.

Table 1 Taxa recorded at GSB and PSB and their nightly mean activity (i.e. the number of one-minute time blocks during which the species/acoustic group was detected as being present per night of recording) during the periods of the survey; the actual numbers of nights of recording are given in brackets.

P1= 1Aug-15Aug; P2= 16Aug-30Aug; P3= 31Aug-14Sep; P4= 15Sep-29Sep

Possibly additional= possible (not sure) activity due to species which could be confused with acoustically similar species of ascertained occurrence in the same minutes (*P. pipistrellus* in the cases ^A and ^B, *E. nilssonii* in the case ^C, other unidentified bats in the case ^D).

^D Activity due to sequences of bad quality, faint calls, probably mostly emitted by *Myotis* bats.

	GSB			PSB			
	P1 (6)	P2 (14)	P3 (9)	P1 (15)	P2 (15)	P3 (15)	P4 (8)
<i>Myotis</i> spp.	0.00	1.43	0.33	5.80	7.20	0.60	0.13

<i>P. kuhlii/nathusii</i>	0.00	1.29	0.33	0.20	0.07	0.73	0.25
<i>P. nathusii/pipistrellus</i>	0.00	0.29	1.00	0.53	0.20	0.20	0.00
<i>P. nathusii</i> possibly additional ^A	0.00	1.07	1.67	0.00	0.00	0.07	0.00
<i>P. pipistrellus</i>	1.83	45.64	42.00	3.87	12.20	3.33	0.25
<i>P. pipistrellus/M. schreibersii/P. pygmaeus</i>	0.00	0.14	0.22	0.00	0.00	0.00	0.00
<i>M. schreibersii/P. pygmaeus</i> possibly additional ^B	0.00	3.43	1.00	0.00	0.00	0.00	0.00
<i>H. savii</i>	0.17	1.71	2.00	0.13	1.00	0.27	0.13
<i>E. nilssonii</i>	4.50	10.29	1.22	2.00	0.13	0.07	0.00
<i>N. leisleri</i>	0.00	0.36	1.11	0.47	0.33	0.27	0.63
<i>N. leisleri/N. noctula/V. murinus/E. serotinus</i> not otherwise identified	0.17	0.57	11.67	0.80	1.53	4.53	0.50
<i>N. leisleri/N. noctula/V. murinus/E. serotinus</i> <i>/E. nilssonii</i>	0.17	0.57	0.56	0.07	0.07	0.00	0.00
<i>N. leisleri/N. noctula/V. murinus/E. serotinus</i> possibly additional ^C	0.00	0.21	0.00	0.00	0.00	0.00	0.00
<i>Plecotus</i> spp.	0.00	0.21	0.00	0.27	0.33	0.20	0.25
<i>B. barbastellus</i>	0.00	0.00	0.11	0.07	0.20	0.33	0.13
CHIROPTERA not otherwise identified ^D	0.00	0.07	0.00	0.73	0.67	0.07	0.13
CHIROPTERA not oth.id. possibly additional ^D	0.00	0.00	0.00	0.13	0.07	0.07	0.00

Influence of weather and period on bat activity

Because of the problems in the specific identification based on echolocation calls, it was impossible to quantify the activity of *P. kuhlii*, *P. nathusii* and, regarding only GSB, *P. pygmaeus* (at PSB we did not detect any activity possibly attributable to this species). The analysis of the activity of the acoustic groups including these species (tab. 1) was avoided, because of no clear biological meaning (being referred to mixed resident and migratory species and, moreover, to small sample sizes).

We took into consideration the identified species/acoustic groups (tab. 1) that belonged to mutually exclusive categories (*Myotis* spp., *H. savii*, *Plecotus* spp., *B. barbastellus*) or that showed an activity almost entirely attributable to mutually exclusive categories (*P. pipistrellus*, *E. nilssonii* and the group *N. leisleri/N. noctula/V. murinus/E. serotinus*, also including in the latter the activity more precisely attributed to *N. leisleri*).

The models for *Plecotus* genus and *B. barbastellus* did not converge, probably due to the limited sample size, and thus results for those taxa are not presented. Nevertheless, the presence of the barbastelle at the two study sites is noteworthy because of the unusual habitat where it was detected (extensively characterized by alpine pastures, prairies and rocks, the nearest woods being located at 1.5 km at GSB and 3 km at PSB), and the recording period, compatible with migration (first detection took place on 13 August and all the other contacts were recorded from 25 August onwards).

The following results relate to the remaining species/acoustic groups and to the general bat activity (Chiroptera activity).

During the nights surveyed, air temperature, wind speed and precipitation varied as summarized in table 2. Bat activity showed a positive relationship with temperature and a negative one with wind speed and precipitation (Appendix X).

Table 2 Weather statistics resulting from the data recorded by the nearest weather stations (locations in Material and Methods) between one hour after sunset and one hour before sunrise during the nights in which the two bat detectors were operational (number of nights in brackets).

P1= 1Aug-15Aug; P2= 16Aug-30Aug; P3= 31Aug-14Sep; P4= 15Sep-29Sep

	Gran San Bernardo			Piccolo San Bernardo			
	P1 (6)	P2 (14)	P3 (9)	P1 (15)	P2 (15)	P3 (15)	P4 (8)
Temperature (°C): min-max	1.1-10.8	0.7-15.6	4.8-11.6	0.8-13.4	2.9-15.4	6.7-12.4	0.0-5.8
Temperature (°C): mean \pm sd	7.7 \pm 2.7	10.3 \pm 3.2	8.8 \pm 1.6	7.9 \pm 3	9.9 \pm 2.6	9.1 \pm 0.8	3.6 \pm 1.5
Total precipitation (mm)	12.6	1.4	8.5	34.8	23.6	13.7	5.3
Precipitation (mm): mean \pm sd	2.1 \pm 5.1	0.1 \pm 0.3	0.9 \pm 2.1	2.3 \pm 7.4	1.6 \pm 4.9	0.9 \pm 2	0.7 \pm 0.9
Wind speed (m/s): mean \pm sd	5.1 \pm 4.8	3.1 \pm 2.6	4.5 \pm 4.8	7.8 \pm 2.6	5.1 \pm 3.0	5.5 \pm 3.3	3.9 \pm 2.5

More precisely, the positive relationship with temperature was significant in all the examined models, except for *H. savii* and *E. nilssonii* at GSB (Appendix II, Appendix Y). For PSB, where the highest mean temperatures were around 13 °C, the results of GLMs show a linear relationship for all the considered species/acoustic groups, with the exception of the group *N. leisleri*/*N. noctula*/*V. murinus*/*E. serotinus*, to which a quadratic relationship provided a better fit. At GSB, the highest mean temperatures reached about 14-15 °C, and quadratic terms fitted the data better in most cases, suggesting that bat activity reached a peak at a mean temperature of 10-12 °C; in the case of the group *N. leisleri*/*N. noctula*/*V. murinus*/*E. serotinus*, there was an evident decrease in activity above the same temperature threshold (see below).

Wind speed was even more frequently correlated with bat activity: with the only exception of *E. nilssonii* at PSB (whose activity did not relate significantly with the variable), all the other species/acoustic groups showed a negative correlation with mean wind speed (Appendix II, fig. 4). In particular, sharp decreases in activity were observed when mean wind speeds exceeded 6 m/s, despite some marginal activity, mainly due to the group *N. leisleri*/*N. noctula*/*V. murinus*/*E. serotinus*, which was recorded up to a mean wind speed of 14 m/s.

During the nights of the survey, precipitation at the two sites was scarce and this probably resulted in a limited association between this variable and bat activity: a significant and negative relationship emerged only for general activity and *P. pipistrellus* at GSB and for the group *N. leisleri*/*N. noctula*/*V. murinus*/*E. serotinus* at PSB (Appendix II, fig. 4).

Bat activity was influenced by period both at GSB and PSB (Appendix II, fig. 3).

For the most part, significant peaks of activity were recorded in the second half of August (P2). At PSB this was the case for *P. pipistrellus*, *H. savii* and of Chiroptera activity; *Myotis* showed maximum activity in the same period both at GSB and PSB, but at GSB the peak was not significant and at PSB the value was similar to that observed in the first part of August (P1), differing significantly only from the values recorded from 31 August throughout September (P3 and P4). At GSB, activity values recorded during the second half of August (P2) for *P. pipistrellus*, *H. savii* and Chiroptera activity were higher than those of the first part of the month (P1), but did not differ significantly from September values (P3). As for *E. nilssonii*, at both sites the activity values were higher in August (P1 and P2) than later (P3), but the difference was significant only for GSB.

The group *N. leisleri*/*N. noctula*/*V. murinus*/*E. serotinus* showed different results both at GSB and PSB: the activity of this group peaked in the period 31 August-14 September (P3), differing significantly from the activity values recorded in any other period.

In order to determine which covariates were more important in explaining the patterns of activity observed for this group, we ran a model combining the significant variables from univariate models. The final model discarded non-significant variables according to Zuur et al. (2009).

At GSB, there was a significant effect of period, wind speed and its quadratic component (tab. 3).

Temperature was not significant. According to the univariate analysis, temperature showed an overall positive correlation with the activity of the group, but the data suggested an inverse relationship at (relatively) higher temperatures. Checking the data set, it emerged that the latter result was influenced by the exceptionally high values of activity of the acoustic group recorded during the nights of 6/7 and 7/8 September, characterized by mean temperatures (7.4 °C) below the average of the period (8.8 °C) and, on the contrary, by the low activity recorded on 23/24 and 24/25 August, when the highest mean temperatures were recorded (around 14 °C) (fig. 5). We conclude that the multivariate model corrects what looks like an anomalous result (the decrease in activity at higher temperatures), indicating that activity was mainly conditioned by period and wind speed rather than temperature.

For PSB, the model indicated precipitation (negatively related), temperature and its quadratic component, and period as factors affecting the activity of the acoustic group (tab. 3).

Table 3 Summary of multivariate GLMs of *N. leisleri*/*N. noctula*/*V. murinus*/*E. serotinus* (Nl/Nn/Vm/Es) group activity index in relation to weather variables (T= mean temperature; P= total precipitation; W= mean wind speed) and period of sampling (P1= 1Aug-15Aug; P2= 16Aug-30Aug; P3= 31Aug-14Sep; P4= 15Sep-29Sep) for GSB and PSB.

GSB	Variable	Estimate	SE	Z	p	Sig
Nl/Nn/Vm/Es	Intercept	0.12612	0.88834	0.142	0.887103	NS
	W	-0.7019	0.20062	-3.499	0.000468	***
	W^2	0.03073	0.01463	2.101	0.035646	*
	P2	1.25382	0.84967	1.476	0.140036	NS
	P3	3.76732	0.85853	4.388	1.14E-05	***
PSB	Variable	Estimate	SE	Z	p	Sig
Nl/Nn/Vm/Es	(Intercept)	-4.10433	1.25565	-3.269	0.00108	**
	T	0.8331	0.27426	3.038	0.002385	**
	T^2	-0.03454	0.01512	-2.284	0.022374	*
	P	-0.19126	0.05607	-3.411	0.000647	***
	P2	0.06668	0.22339	0.298	0.765325	NS
	P3	1.01352	0.20293	4.994	5.90E-07	***
	P4	1.53846	0.4984	3.087	0.002023	**

Therefore, at both sites, there was significant variation in activity according to period and the timing of the activity peaks distinguished this acoustic group from the other bats, which showed different activity patterns. Moreover, during the nights of the peak period, the proportion of activity of *N. leisleri*/*N. noctula*/*V. murinus*/*E. serotinus* recorded in the central part of the night was comparatively higher than that observed for the other bats; in the case of GSB the difference was significant (fig. 5). Finally, only 3 feeding buzzes were observed in the echolocation sequences of the acoustic group during the entire period at the two sites.

Discussion

A full understanding of bat migration behavior and the identification of migration routes are difficult yet important goals for bat conservation, particularly regarding the aim of preventing negative effects caused by the creation of wind farms and, more generally, for the implementation of the EUROBATs agreement. Here, we show evidence of bat migration through the Western Italian Alps.

According to the literature (Fleming and Eby 2003; Hutterer et al. 2005; Dietz and Kiefer 2014), most bat species detected at GSB and PSB are sedentary or partly sedentary, but at least one species

recorded, *N. leisleri*, is known to carry out long migrations across Europe (see appendix III for a more detailed discussion).

At GSB and PSB, significant variations in bat activity were negatively related to wind speed, positively related to air temperature and, to a lesser extent, negatively related to precipitation. Similar relationships between bat activity and meteorological variables are well documented in the literature (e.g., Erkert 1982; Erickson and West 2002; Reynolds 2006; Cryan and Brown 2007; Horn et al. 2008; Arnett et al. 2008; Baerwald and Barclay 2011).

Bats markedly lowered their activity in the presence of wind speeds higher than 6.0 m/s, as previously reported in case studies at wind farms (e.g.: Reynolds 2006; Arnett et al. 2008; Horn et al. 2008; Korner-Nievergelt et al. 2013; Voigt et al. 2015).

Bat activity increased linearly for mean temperatures below 10-12°C, while between the same threshold and the highest values of mean temperature recorded during the survey (13 °C at PSB, 14-15 °C at GSB) a tendency to interrupt the increase in activity was observed for *P. pipistrellus* at GSB and for *N. leisleri*/*N. noctula*/*V. murinus*/*E. serotinus* both at PSB and GSB.

Such observations are largely consistent with published knowledge on bat physiology and the availability of their prey in cold climates: low temperatures raise the energetic costs of bat activity (Racey and Speakman 1987) and, at the same time, they negatively influence the availability of insect-prey (Cockbain 1961; Williams 1961; Taylor 1963; Lewis and Taylor 1965; Alma 1970; Jones et al. 1995). In northern Scandinavia, the availability of aerial insects sharply declined below 14 °C, while they were found to be constantly abundant for temperatures ≥ 14 °C (Speakman et al. 2000). Likewise, increases in bat activity should be expected to stop when an optimal (relative to the area) value of temperature is reached.

The data recorded at GSB for *N. leisleri*/*N. noctula*/*V. murinus*/*E. serotinus* appear to be partially in contrast to these considerations, suggesting a decrease in the activity of the group at increasingly higher temperatures, but further analysis demonstrated that this result was a consequence of the pre-eminent role of other factors, in particular the period, in explaining the activity of the group.

In both sites, the activity peaks of the identified species/acoustic groups mainly occurred in the second half of August. Only the group *N. leisleri*/*N. noctula*/*V. murinus*/*E. serotinus* showed a maximum of activity, significantly different from the values recorded in all the other periods, from 31 August to 14 September. Taking into account the period, the fact that the echolocation sequences of the group that could be identified at species level were attributed to *N. leisleri* (a long-distance migratory bat), the activity peak of the group in the central part of the night (tendentially later than observed for the other bats) and the characteristics of the calls (clear predominance of QCF calls, almost total absence of feeding buzzes), we conclude that a late-summer migratory flow passes through GSB and PSB and that at least one species – *N. leisleri* – is involved.

Present knowledge concerning the migratory movements of this species across Italy is very limited. The species is present in the country throughout the entire year and some evidence of its reproduction has been reported for northeast (Niederfriniger 2001) and central Italy (Ancillotto and Russo 2015); most records, however, are collected in migratory periods or in winter.

Females are reported to reach a mating area located in the Northern Apennines (central Italy) in late August/early September (Vergari and Dondini 2011); a female banded at the same site was later recaptured within a nursery in Poland, proving the occurrence of migration between the two areas (Dondini et al. 2012).

In Piedmont, in the plain area of La Mandria Park, lesser noctules, comprising a few females, are already present in June, but their number (monitored thanks to the use of bat boxes) increases from the middle of August to reach a maximum in September (P. Debernardi and S. Lacaria, unpublished data). Similar data are reported in Switzerland for Canton Ticino, where the first females are observed in bat boxes during the second half of August (Zambelli et al. 2008).

According to long-term mist-netting results, at Col de Bretolet (1923 m a.s.l.; canton of Valais) male and female lesser noctules transit, with few exceptions, from the middle of August to the end

of September, with a peak at the beginning of September; at Col de Jaman (1512 m; Vaud Prealps) the passage begins around the middle of August, has its maximum at the end of August-beginning of September, and, probably thanks to the low elevation, continues until the end of October (Oppliger 2004).

Temporal variations in the activity of the *N. leisleri*/*N. noctula*/*V. murinus*/*E. serotinus* group at the two study sites are in agreement with the above data, although they did not allow the determination of the end of migratory flow. The data recorded in the second half of September, available only for PSB, showed a general decrease in the activity of the group. Nevertheless, it is impossible to say if the migration came to an end, or if it was just temporarily interrupted, since the period was characterized by an abrupt decrease in temperatures coincidental with a decrease in general bat activity.

Another unanswered question regards the increase in the activity of the acoustic group observed at GSB at the beginning of September, larger than that recorded at PSB: it might indicate that some bats that entered the region remained to winter in the Aosta Valley, or that they continued the migration along different routes; the available data are in any case too scarce to draw any conclusions on the question.

Nevertheless, the data recorded add evidence to previous records suggesting that *N. leisleri* can migrate across the Alps, transiting at high elevation (Zingg and Bontadina 2016; Widerin and Reiter 2017; Patriarca et al. 2018), which includes the finding of a dead individual of the species on an alpine glacier at 2,600 m a.s.l. (Aellen 1962).

Because of identification problems, it is not possible to draw conclusions concerning the other species of the same acoustic group that are known to migrate over long distances, i.e. *N. noctula* and *V. murinus*. However, the occurrence of the latter seems more likely because the species, contrary to *N. noctula*, has already been recorded in the Aosta Valley (Patriarca and Debernardi 2014).

Some social calls of *P. nathusii*, the other long distance migrating bat species, were recorded during the survey a little below GSB, proving without any doubt the presence of this species in the Aosta Valley, which was previously only conjectured (Patriarca and Debernardi 2014). It is not possible to draw conclusions about the presence of *P. nathusii* at GSB and PSB because of the problems in identification of its echolocation calls, whose characteristics largely overlap with those of the calls emitted by *P. pipistrellus* and *P. kuhlii*. The latter species, despite being primarily a low altitude bat (Lanza 2012; Dietz and Kiefer 2014), was recorded at both study sites, reaching the highest elevation so far ascertained in Italy at GSB (2208 m a.s.l.).

Nevertheless, at GSB and PSB the activity referable to all the acoustic groups possibly comprising *P. nathusii* was limited, suggesting that if a migration flow of this species does exist at the two passes, it is either marginal or takes place later in the season, in periods that were not considered in the survey. At Col de Bretolet, *P. nathusii* mainly transits from the end of August to the end of September, and at Col de Jaman, the passage of this species, likely favored by the lower elevation, peaks about one month later and is much more intense (Oppliger 2004).

The presence of *P. pygmaeus*, rarely recorded in the Aosta Valley (Debernardi and Patriarca 2008; Patriarca and Debernardi 2014) and possibly a migratory bat, was not detected at PSB, while at GSB, some acoustic sequences probably emitted by individuals of this species were conservatively attributed to the group *P. pipistrellus*/*M. schreibersii*/*P. pygmaeus*.

Finally, concerning the species that are usually considered of stationary habits, it remains to be ascertained if the presence of *B. barbastellus*, recorded at both study sites, represents a case of ecological adaptation of this primarily forest species to open habitat types (as demonstrated for a coastal habitat in Central Italy: Ancillotto et al., 2012), or whether it is the result of migratory movements, which may pass through unfavorable habitat types, like sea areas. Widerin and Reiter (2017) recorded this species at two high elevation sites (2250 and 2315 m) in the Central Alps and one barbastelle was captured in the Orco Valley (Gran Paradiso National Park, Western Alps) in conditions similar to those recorded in this study with regard to the environment (open alpine

habitat), the elevation (2292 m) and the period (middle of August) (Patriarca et al. 2018). According to the review by Hutterer et al. (2005) “barbastelles are sedentary bats but may occasionally migrate or disperse”.

The present conclusions were conditioned by the limited survey effort performed and the interruptions in recording at GSB. Getting a clearer comprehension of bat migration at the study sites would require more surveys, extending the recording period (weather conditions and accessibility allowing) to October, operating from more recording points for each site and (to take into account possible annual variations) for more years.

Enlarging the data set would allow to gain an increased understanding of the influence of weather variables on migration, and particularly the role of wind speed combined with wind direction, which can have important implications for bat migration (Shamoun-Baranes et al. 2007; Smith and McWilliams 2016, Hüppop and Hill 2016).

Nowadays, the possibility to record bat calls using bat detectors that operate in real-time and can be left unattended for several days gives the opportunity to collect useful information on bat migration in a non-invasive way, including at sites, such as high mountain areas, where direct (manual) surveys may prove difficult because of accessibility and environmental factors. The problem of the correct identification of many species through acoustic analysis is still unsolved (Russo and Voight 2016); nevertheless, even adopting a very conservative approach as here – despite not being able to identify many species – it is possible to get useful information to improve the knowledge of bat migration.

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