



The use of solar farms by bats in mosaic landscapes: Implications for conservation

Kriszta Lilla Szabadi^a, Anikó Kurali^b, Nor Amira Abdul Rahman^c,
Jérémy S.P. Froidevaux^{d,e,f}, Elizabeth Tinsley^f, Gareth Jones^f, Tamás Görföl^{g,h},
Péter Estókⁱ, Sándor Zsebők^{c,j,*}

^a Hungarian University of Agriculture and Life Sciences, H-2100 Gödöllő, Hungary

^b Fertő-Hanság National Park Directorate, H-9435 Sarród, Hungary

^c Department of Systematic Zoology and Ecology, ELTE, Eötvös Loránd University, H-1117 Budapest, Hungary

^d University of Stirling, Biological and Environmental Sciences, Faculty of Natural Sciences, Stirling, UK

^e Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, 75005 Concarneau, Paris, France

^f School of Biological Sciences, University of Bristol, Bristol BS8 1TQ, UK

^g National Laboratory of Virology, University of Pécs, H-7624 Pécs, Hungary

^h Department of Zoology, Hungarian Natural History Museum, H-1088 Budapest, Hungary

ⁱ Department of Zoology, Eszterházy Károly Catholic University, H-3300 Eger, Hungary

^j Centre for Ecological Research, Institute of Ecology and Botany, H-2163 Vácrtót, Hungary

ARTICLE INFO

Keywords:

Chiroptera
Habitat loss
Solar panels
Renewable energy
Anthropogenic effect
Anthropocene

ABSTRACT

Solar energy is an important renewable energy source. However, the ecological effects of solar farms are largely unknown. Behavioral experiments proved previously that smooth surfaces, such as solar panels act as sensory traps for bats and insects, increasing collision risk, and suggesting that solar farms may affect local ecosystems in a complex way. As the orientation of bats is impeded around smooth surfaces, the exploitation of solar farms as foraging habitats by bats needs research. We surveyed the activity of bats at solar farms and in the neighboring habitats (forests, grasslands, arable fields, settlements and watersides) to evaluate the effects of solar farms on the occurrence and activity of bats and on the composition of bat communities. We conducted bioacoustic surveys at 190 sites in 15 areas of Hungary and recorded nearly 30 000 bat echolocation call sequences. We detected patterns of overall bat activity similar to those in other open habitats such as arable land and grassland indicating that some bat species can exploit this anthropogenic environment. Bat species detected at solar farms also frequently occur in arable land and settlements (*Hypsugo savii*, *Nyctalus noctula* and *Pipistrellus kuhlii*), suggesting that bats adapted to anthropogenic environments exploit solar farms. However, some species of major conservation concern (e.g. *Myotis* spp. and *Barbastella barbastellus*) were detected less frequently on solar farms than in other habitats raising implications for mitigation procedures.

* Correspondence to: Alkotmány Road 2–4, H-2163 Vácrtót, Hungary.

E-mail address: zsebok.s@gmail.com (S. Zsebők).

<https://doi.org/10.1016/j.gecco.2023.e02481>

Received 16 February 2023; Received in revised form 18 April 2023; Accepted 19 April 2023

Available online 20 April 2023

2351-9894/© 2023 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Global ecosystems have been significantly transformed by humans, through changes in factors such as the composition of the atmosphere, the climate, the land surface, and overexploitation and conversion of habitats. The extent and longevity of these changes suggest that the Earth may have reached a new geological epoch, which has been dominated by humans and termed the Anthropocene (Lewis and Maslin, 2015; Waters et al., 2016). Organisms tolerate human-induced changes to varying degrees: many taxa experience dramatic population declines, potentially contributing to a sixth wave of mass extinction on our planet, while others tolerate human activities and even thrive in anthropogenic habitats (Filgueiras et al., 2021; Voigt and Kingston, 2016). Bats are especially affected by anthropogenic changes (Voigt and Kingston, 2016; Frick et al., 2019). Over 15% of c.a. 1400 bat species are considered threatened by the IUCN (International Union for Conservation of Nature) and a further 18% of bats are “Data Deficient” indicating that considerable research effort is needed to reveal the potential anthropogenic factors affecting population changes of bats (Browning et al., 2021).

Land cover modification and habitat loss are some of the main drivers of bat population declines worldwide (Avila-Flores and Fenton, 2005; Browning et al., 2021; Frick et al., 2019). Forests are often key habitats for protecting the local abundance and global diversity of bats (Frick et al., 2019); nevertheless, forestry treatments strongly influence bats’ foraging opportunities and roost availability (Carr et al., 2020). Moreover, almost 40% of terrestrial land has been transformed into agricultural cultivation worldwide (Frick et al., 2019). Urbanization also significantly affects bats, putting differential selection pressure on different bat species through habitat loss, light and noise pollution (Boldogh et al., 2007; Duvergé et al., 2000; Frick et al., 2019; Russo and Ancillotto, 2015; Stone et al., 2015). Additionally, in the last decade, novel anthropogenic challenges have been created for bats by populating fields with artificial installations such as solar panels that cover large parts of the landscape.

In order to reduce carbon emissions and hence combat climate change, a universal goal is to expand the use of green energy sources worldwide (Harrison et al., 2017; Jaeger-Waldau, 2019). Until the late 2000s, wind energy was chosen as the major source of renewable energy. However, it has resulted in some negative impacts on wildlife such as habitat loss and barrier effects (Barré et al., 2018; Dahl et al., 2012; Drewitt and Langston, 2006; Voigt et al., 2012). The most severe problem for bats and birds is the high mortality rate caused by wind turbines installed on upwind slopes or close to their migratory routes (Alvarez-Castañeda, Lidicker, 2015; Baerwald et al., 2008; Cryan et al., 2014; Wieringa et al., 2021). Birds and bats often collide with moving blades, and in the case of bats, mortality is also caused by barotrauma - tissue damage of the lungs caused by the rapid reduction in air-pressure near to the moving turbine blades (Alvarez-Castañeda, Lidicker, 2015; Baerwald et al., 2008; Cryan and Barclay, 2009; Cryan et al., 2014). In the last decade, photovoltaic (PV) solar farms have increased rapidly in their presence globally due to the improved efficiency and reduced costs of hardware, and because excess electricity can be sold to the grid (Harrison et al., 2017). The on- and off-grid capacity for solar energy expanded from 70 GW a decade ago to 942 GW in 2021 (REN21 Report, 2022). Onshore wind farms and PV solar farms have some similarities, for example, both need large areas of land in order to maximize the energy yield from their respective resources, and both require infrastructure to transport the large amount of electricity generated to the place of consumption (Harrison et al., 2017). These facilities can cover large areas and potentially have major ecological impacts (Hernandez et al., 2014), however to our best of knowledge no scientific study has been published yet about the effects of solar farms on bats.

Besides the potential habitat loss for foraging bats, PV solar farms may also create challenges to wildlife by presenting large areas of smooth surfaces. Although the specific effect of solar panels on bats is still unknown, Grief and Siemers (2010) found that bats perceive horizontal, smooth surfaces (acoustic mirrors) as water due to their similar echo-acoustic properties. This behavior seems to be phylogenetically widespread and innate among echolocating bats, as juveniles also try to drink from the artificial smooth surfaces. Echolocation is the main way to recognize water surfaces and takes dominance over conflicting sensory information provided by e.g., vision, olfaction, touch and taste. Also, bats perceive vertical smooth surfaces as open flyways, causing collisions and potential injuries (Grief et al., 2017). Moreover, bats sometimes collide with smooth surfaces of 45 degrees and suffer serious injuries (Ingeme et al., 2018). It is conceivable that bats may find it difficult to orient at solar farms potentially resulting in avoidance or low usage of these artificial habitats.

The smooth surfaces of solar panels attract aquatic insects, because their polarization pattern is similar to that of water (Horváth et al., 2009). PV solar cells are a potent source of polarized light pollution; a type of light that attracts most flying aquatic insects (Horváth et al., 2010; Száz et al., 2016). Attraction to polarized light is adaptive for many species of aquatic insect (Száz et al., 2016), helping them to locate water bodies suitable for laying eggs (Horváth et al., 2010). It might be hypothesized that these greater abundances of insect prey could be advantageous for bats, hence PV solar farms may function not only as ecological traps for wildlife but may also affect ecological systems in complex ways (Chock et al., 2021).

In this study, we aimed to analyze the ecological effects of PV solar farms on insectivorous bats. Using passive acoustic surveys, our objectives were to (i) characterize the usage of solar farms by bats and (ii) compare species composition, abundance and foraging activity between solar farms and other nearby habitats including forests, grasslands, arable fields, settlements and watersides in mosaic landscapes. In general, we predicted that the solar farms provide challenging orientation cues for bats, and therefore the activity of bats will be lower here than in the neighboring habitats. In addition, we predicted that the effect of solar farms would be species-specific: those bat species that can overcome potential orientation problems (e.g. by flying high) and that can exploit any food sources enhanced at solar farms will be relatively more abundant than other bat species. Accordingly, we predicted substantial differences in bat community composition between solar farms and semi-natural habitats such as forests and watersides, but none with other human-altered habitats including arable lands and settlements.

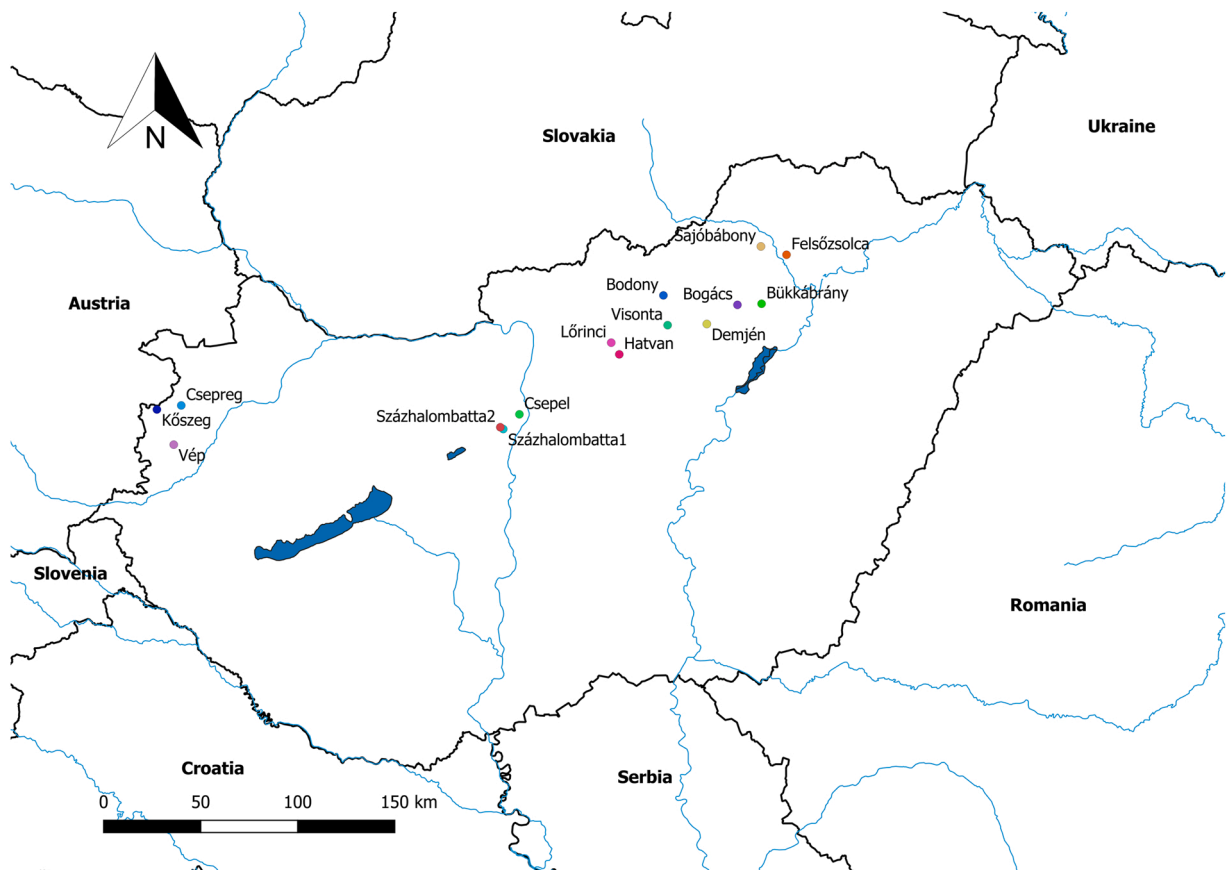


Fig. 1. Map of the sampling areas in Hungary. The different colors mark the different sampling areas; the name of the nearest settlements are indicated.

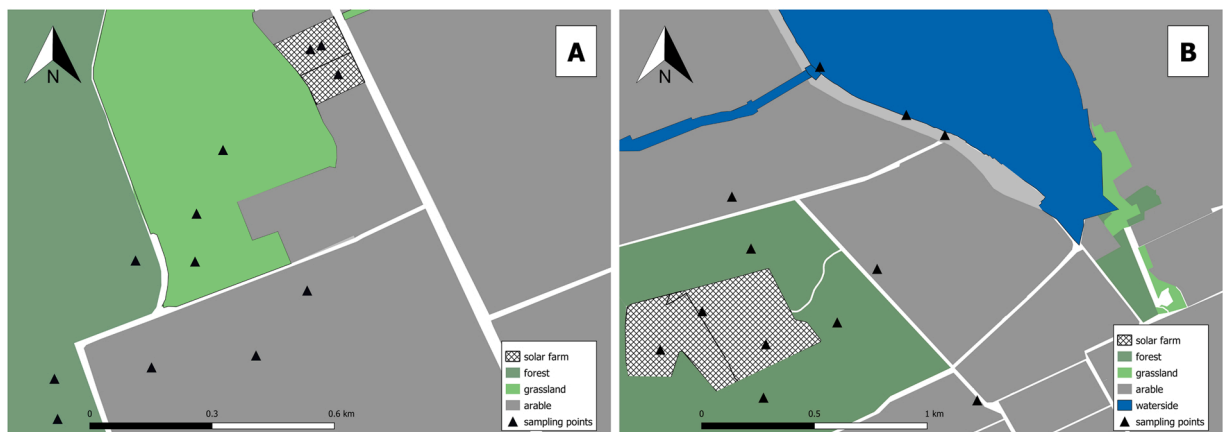


Fig. 2. Detailed map of two representative sampling areas. Two examples selected from our sampling areas: (A) Bogács, (B) Visonta. White lines represent roads.

2. Material and methods

2.1. Data collection

The study was carried out at 15 sampling areas in mosaic landscapes of Hungary (Fig. 1). We chose the areas in a way to cover a large geographic range in the country, so they were relatively distant from each other, and contained a range of different habitats. The

average distance between the nearest sampling areas was 11.8 ± 5.3 km (mean \pm SD); the largest distance was 335.9 km. Each sampling area involved one solar farm and further sampling places in different habitats (control habitats) available around the 5 km radius of the solar farms (Table A1). In each habitat, we determined 1–6 sampling points (3.6 ± 1.3 in average) depending on the size of the given habitat surveyed within the given sampling area (Fig. 2). Altogether, we collected data from 190 sampling points. The mean distance between the nearest sampling points was 0.20 ± 0.17 km. The sampling points of a given habitat were 0.119 ± 0.096 km from the edge of other habitats. The mean distance between the solar farms and the nearest settlement boundary was 0.3 ± 0.5 km (minimum 0 km, maximum 1.75 km).

We sampled solar farms of a range of sizes (between 1.2 and 45 ha), where the vertical angle of the solar panels was between 0 and 35 degrees (Table A2). The main land-use types recognized for control habitats were forests, arable lands, grasslands, settlements and waterside. Forest habitats included coniferous, mixed coniferous-oak, and oak (*Quercus*) forests, and black locust (*Robinia pseudoacacia*) plantations in which we made recordings in the forest roads. Maize, sunflower, apple tree, soy, wheat plantations, vineyards and freshly harvested fields were classified as arable lands. Grasslands included meadows, pastures, grass yards and scrub meadows. In settlements, we sampled mainly green areas such as streets aligned with trees, parks, and cemeteries. Waterside habitats were located beside large rivers and fishponds.

We conducted the acoustic sampling between 5th of July and 16th of September in 2020. We sampled each area only once with one sampling night in each sampling point. The different habitats within the areas were sampled in the same night. The acoustic recordings started at sunset and lasted for 4 h. We used AudioMoth (Hill et al., 2018; v.1.1.0) full-spectrum acoustic devices to record the calls of bats. The sampling frequency was 256 kHz; gain was set to medium; the recording chunks were 295 s long with 5 s sleep to save the files. We conducted the sound recordings for one night at each sampling point. The recordings were made in favorable weather conditions, i.e. on windless nights without rain. The average temperature of the sampling places at the time of the recordings was 23.6 ± 3.8 °C.

2.2. Sound analysis

First, we automatically searched the bat calls on the recordings by using the program Bat Detective (Mac Aodha et al., 2018) and then cut the sequences out from the recordings with a self-written script in R (R Core Team, 2019; script available upon request from the authors). We defined a sequence as a series of echolocation calls with inter-pulse interval between calls less than 3 s. The sequences were examined manually using the Kaleidoscope Pro program (Wildlife Acoustics, Inc.). Species identification was carried out based on frequency and time measurements in the literature (Obrist et al., 2004; Papadatou et al., 2008; Pfaller and Kusch, 2003; Russo and Jones, 2002; Walters et al., 2012). We successfully identified the following species: *Barbastella barbastellus*, *Hypsugo savii*, *Pipistrellus pipistrellus*, *P. pygmaeus*, *Nyctalus noctula* and *N. leisleri*.

In addition to the species-level identification, species groups were also formed, where the spectrographic characteristics of several bat species can overlap and species-level identification can be ambiguous. Accordingly, we constructed three groups: (1) *Myotis* spp., including all *Myotis* species from Hungary characterized by steep frequency modulated signals. Many of these species use broadband echolocation calls that are adapted for foraging in confined spaces such as woodland interiors, and are categorized as ‘short-range echolocators’ (Frey-Ehrenbold et al., 2013); (2) *P. kuhlii/nathusii* or *Pipistrellus kuhlii* and *P. nathusii* because their characteristics largely overlap and both species occur in Hungary. These bats emit broadband calls with narrowband tails and often forage along habitat edges such as treelines – they can be categorized in the guild of ‘medium-range echolocators’ (Frey-Ehrenbold et al., 2013); and (3) a so-called QCF group for species with quasi-constant frequency signals in the frequency range of 23–31 kHz potentially including *Eptesicus serotinus*, *N. leisleri*, *N. noctula* and *Vespertilio murinus*. The narrowband calls emitted by these species are adapted for foraging in open spaces, and the bats can be classified in the guild of ‘long-range echolocators’ (Frey-Ehrenbold et al., 2013). We have to note that the limited sensitivity of the Audiomoth device at high frequencies restricts the bandwidth of sound recordings and contributed to our decision to handle the *Myotis* species together. Additionally, we identified the social calls from the sequences assigned to *P. kuhlii/nathusii* group to interpret the results, but we did not use it in the statistics, because they occurred only at 10 sampling sites.

We also registered the occurrence of terminal ‘feeding’ buzzes characterized by rapid increases in the rate of echolocation calls (Ratcliffe et al., 2013) indicating prey capture attempts.

2.3. Statistical analysis

We used bat activity as a proxy of bat abundance because it was not possible to differentiate individuals using passive acoustic sampling. Activity was defined as the sum of the sequences recorded over a night. For each sampling point, we calculated the activity by species or species group. Moreover, regardless of the species, we obtained the overall activity. For further statistical evaluations, we excluded the data from *B. barbastellus* (55 sequences) and feeding buzzes (197 sequences) as few of these sounds were recorded and therefore not sufficient for the statistical modelling. The recording rate of feeding buzzes is typically lower (e.g.: Russo and Jones, 2003) because in contrast to the continuously emitted echolocation sounds, bats emit feeding buzzes only when determining the exact location of the prey. Furthermore feeding buzzes typically consist of low intensity call sequences which makes it difficult to record them.

To compare the activity of bats in solar farms versus other habitats, we built Generalized Linear Mixed Models (GLMM) with negative binomial error distributions for each activity variable as a response variable (nine models overall). We included the habitat type and month as fixed factors, and temperature as a continuous fixed effect. We also included the area and the habitat within the area as random effects to control for the spatial dependency of the sampling points both within and between the areas. Statistical analyses

Table 1
Bat occurrences by habitat.

	Solar farm (N = 54)	Forest (N = 32)	Arable field (N = 46)	Grass-land (N = 21)	Settlement (N = 27)	Waterside (N = 10)	Total (N = 190)
<i>B. barbastellus</i>	0 (0.00)	49 (12.5)	5 (10.9)	1 (4.8)	0 (0.0)	0 (0.0)	55 (5.3)
<i>H. savii</i>	307 (79.6)	21 (28.1)	253 (67.4)	51 (71.4)	1735 (88.9)	160 (90.0)	2527 (69.0)
<i>Myotis</i> spp.	12 (11.1)	137 (34.4)	29 (23.9)	34 (38.1)	8 (14.8)	10 (20.0)	230 (22.1)
<i>N. leisleri</i>	97 (64.8)	77 (21.9)	113 (58.7)	33 (47.6)	50 (63.0)	52 (80.0)	422 (54.7)
<i>N. noctula</i>	1860 (98.2)	327 (56.3)	1509 (95.7)	1104 (95.2)	1723 (74.1)	383 (100.0)	6906 (86.8)
<i>P. kuhlii/P. nathusii</i>	1586 (100.0)	371 (53.1)	1409 (97.8)	472 (90.5)	3487 (100.0)	4510 (100.0)	11835 (90.5)
<i>P. pipistrellus</i>	53 (37.0)	179 (43.8)	77 (47.8)	60 (81.0)	282 (55.6)	315 (60.0)	966 (49.5)
<i>P. pygmaeus</i>	57 (31.5)	294 (40.6)	32 (39.1)	378 (81.0)	47 (37.0)	271 (40.0)	1079 (41.6)
QCF group	411 (90.7)	509 (78.1)	595 (97.8)	208 (100.0)	498 (81.5)	416 (100.0)	2637 (90.5)
feeding buzz	32 (33.3)	34 (21.9)	41 (43.5)	45 (57.1)	23 (40.7)	22 (70.0)	197 (39.5)
all detected sequences	4786	2459	4361	2689	9041	6517	29853

The number of detected bat sequences (above) and the percentage of the sampling points where the sequence occurred (below, in brackets). The number of sampling points are indicated in the header of each column.

were carried out with the `glmer.nb` function of 'lme4' package (Bates et al., 2015) in R, and the output of the summary function was used to generate the statistical results. To control for the multiple comparisons, we tested the differences of bat activity between the solar farms and the other habitats with Dunnett's post-hoc test using the `glht` function of the 'multcomp' package (Hothorn et al., 2008). The boxplots were generated by the `ggplot2` package (Wickham, 2016). Model validation was conducted using the 'DHARMA' package (Hartig, 2021). We also examined spatial autocorrelation of model residuals using Moran's I statistic 'spdep' package; (Bivand, 2020) and found no significant spatial autocorrelation ($P > 0.10$). To assess goodness-of-fit, we calculated marginal and conditional R^2 for each model using 'MuMin' R package (Bartoń, 2020). We present the result of the full model and provide the Akaike information criterion (AIC) for both full and null models.

To explore the habitat use of bats on community level, we also conducted a multivariate exploratory analysis. With the help of the 'vegan' package (Oksanen et al., 2016), we applied non-metric multidimensional scaling (NMDS) using the function `metaMDS` based on the logarithmic transformed data of the number of the sequences of the species and species groups (9 variables). Five NMDS dimensions were generated for which the calculated stress value was 0.081, thus indicating good fit. Through this ordination, habitat types can be visualized in low-dimensional space according to their similarity in species composition. We evaluated visually the similarity of bat communities of the different habitats by the overlap of point clouds.

3. Results

We recorded 29 853 bat call sequences and identified six species and three species groups, and additionally, feeding buzzes at the 190 sampling sites in the 15 sampled areas (Table 1). The smallest number of sequences were from *B. barbastellus* that occurred mostly in forest, but also in the arable and grassland habitats. All other species and species groups were recorded in all habitat types. Calls belonging to the *P. kuhlii/nathusii* group were the most abundant (11 835 sequences) followed by *N. noctula* (6906 sequences). Altogether, we recorded 197 feeding buzzes.

At the solar farms, we identified all the species and species groups documented except for *B. barbastellus*. *P. kuhlii/P. nathusii* and *N. noctula* occurred at over 98% of the sample points in the solar farms (Table 1). Calls belonging to the QCF group, *H. savii* and *N. leisleri* were also present in more than 50% of the sampling points in this habitat type. Feeding buzzes were also detected at solar farms from different species: 14 from *P. kuhlii/P. nathusii*, 10 from *N. noctula*, two from *H. savii* and QCF group and one from *P. pygmaeus*.

The number of detected sequences showed significant differences between solar farms and the other habitat types for several bat species (Fig. 3 and Table 2). Compared to solar farms, the activity of *H. savii*, *P. kuhlii/P. nathusii*, *N. noctula* was significantly lower in forest while *Myotis* spp. activity was significantly higher. We found significantly higher activity of *Myotis* spp. and a trend for higher activity of *P. pygmaeus* on grasslands than at solar farms. The number of detected sequences from the settlements showed significantly more activity from *H. savii*, *P. kuhlii/P. nathusii*, *P. pipistrellus*, and for the overall number of bat sequences compared to the solar farms. At waterside habitat, we also recorded a significantly higher number of bat sequences for *P. kuhlii/P. nathusii*, *P. pipistrellus*, QCF group and for the overall bat activity than at solar farms. We found no significant differences in bat activity between the arable fields and solar farms. To further investigate the *P. kuhlii/P. nathusii* group, social calls of *P. kuhlii* were identified from 2 solar farms, 2 watersides,

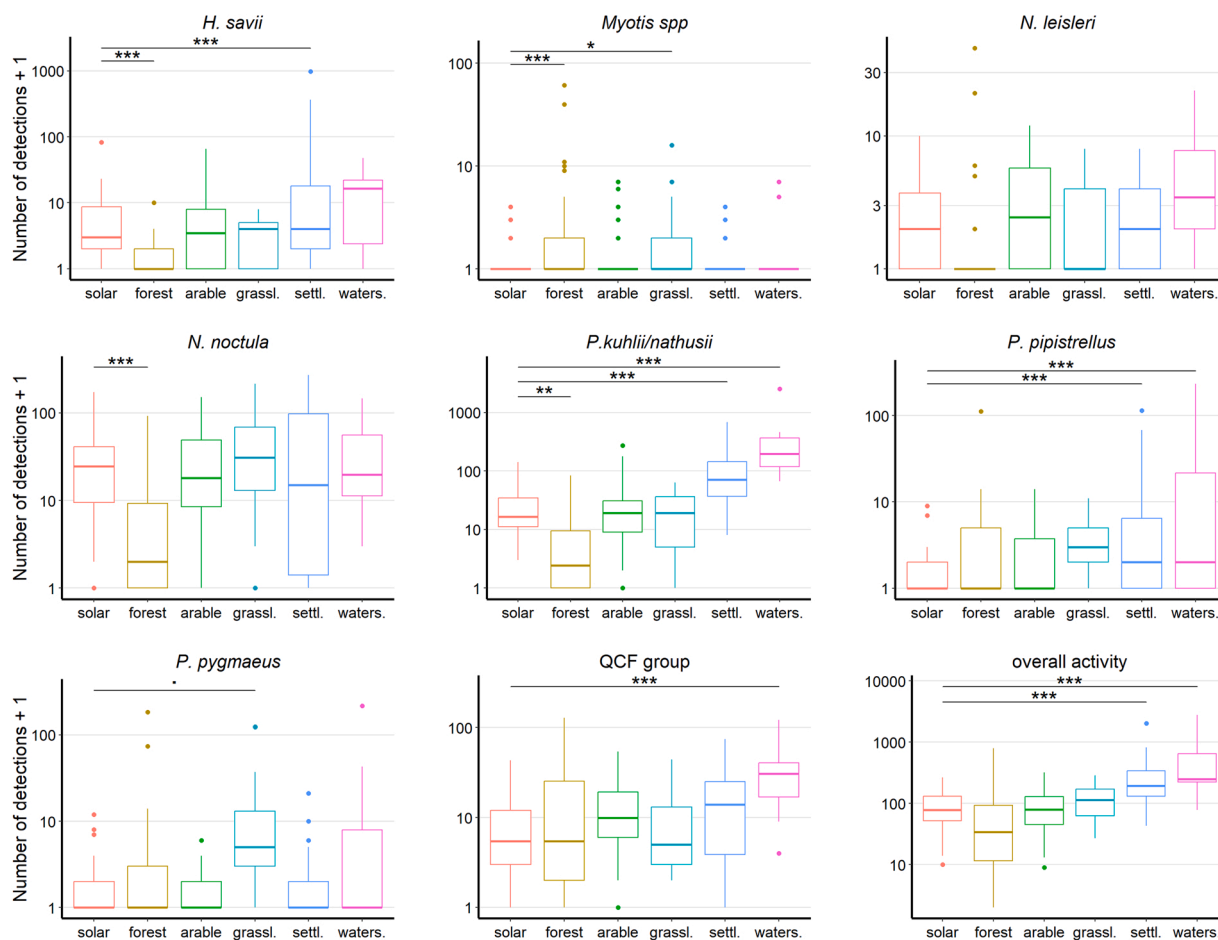


Fig. 3. Number of detections of bat sequences in the different habitats. The colors indicate the habitats. We tested the differences in the number of detections only between the solar farms and the other habitats. Note that we had different number of areas with the given habitat, see Table A1 for more information. Also, note that the vertical axis is in logarithmic scale and the maximum values are different on the plots (solar – solar farm, grassl. – grassland, settl. – settlement, waters. – waterside). The detailed statistical results are available in Table 2.

2 grassland habitats and 3 settlements, while social calls of *P. nathusii* were detected in 2 watersides and 1 arable habitats but none at solar farms.

Based on the visual inspection of the NMDS results, we found large overlap in the distribution of sampling points referring to the bat communities from different habitats (Fig. 4). The bat communities of solar farms and agricultural habitats were the most similar as the center of these habitats' point clouds were the closest and the overlap of the point clouds were the largest in the NMDS space.

4. Discussion

We may expect that solar farms are suboptimal habitats for bats because these are frequently situated in homogeneous fields without any natural linear features for orientation. As we found a considerable amount of activity for several bat species at solar farms, we can infer that orientation is not a problem in the vicinity of the solar panels for many bats. While solar panels can function as acoustic mirrors and reflect away the echoes from the bats when bats approach the surface at an acute angle (Greif and Siemers, 2010; Greif et al., 2017), the other side of the installations (usually metal constructions at the back of the panels) may provide sufficient cues for orientation. This is further supported as we registered not only species that usually fly at high altitude such as *Nyctalus* spp. and species using low frequency QCF signals (Ciechanowski, 2015; Dietz and Kiefer, 2016), but also *Pipistrellus* spp. that usually commute at lower height at the edges of cluttered habitats including along tree lines and hedgerows (Ciechanowski, 2015; Dietz and Kiefer, 2016).

The detection of feeding buzzes at solar farms proved that bats not only commute over this habitat but also forage there. We expect two main sources of insects at solar farms. First, the solar farms we sampled usually had some herbaceous, low height undergrowth that might be a suitable habitat for several flying insect taxa including Hymenoptera, Sternorrhyncha, Lepidoptera and small dipteran insects such as Brachycera, and Orthoptera (Báldi et al., 2013; Bonari et al., 2017) that may provide food for bats (Dietz and Kiefer,

Table 2

Estimated model parameters ($\beta \pm$ SE) and test statistics (Z and P values) from the GLMMs built for habitat comparisons with solar farms.

		<i>H. savii</i>	<i>Myotis spp.</i>	<i>N. leisleri</i>	<i>N. noctula</i>	<i>P. kuhlii/nathusii</i>	<i>P. pipistrellus</i>	<i>P. pygmaeus</i>	QCF group	all
forest	β	-2.06	2.61	-0.53	-1.41	-1.07	1.12	1.34	0.52	-0.30
	SE	0.56	0.72	0.49	0.38	0.33	0.56	0.91	0.35	0.25
	Z	-3.68	3.65	-1.09	-3.73	-3.20	2.02	1.46	1.48	-1.23
	P	< 0.001	< 0.001	0.81	< 0.001	0.007	0.17	0.46	0.43	0.77
arable	β	0.05	0.79	0.15	-0.44	-0.02	0.37	0.08	0.49	-0.03
	SE	0.46	0.68	0.41	0.33	0.29	0.51	0.74	0.30	0.22
	Z	0.11	1.16	0.36	-1.32	-0.08	0.72	0.11	1.64	-0.14
	P	1.00	0.74	0.99	0.62	1.00	0.93	1.00	0.33	1.00
grassland	β	-0.25	2.05	0.21	0.63	-0.12	0.98	2.56	0.53	0.30
	SE	0.60	0.85	0.57	0.46	0.39	0.64	1.13	0.43	0.28
	Z	-0.41	2.42	0.36	1.37	-0.32	1.52	2.26	1.24	1.05
	P	1.00	0.03	0.99	0.51	1.00	0.43	0.08	0.58	0.20
settlement	β	1.96	1.18	0.24	-0.50	1.63	2.22	0.21	0.78	1.34
	SE	0.53	0.96	0.48	0.39	0.34	0.61	0.92	0.35	0.25
	Z	3.69	1.23	0.50	-1.28	4.81	3.63	0.23	2.22	5.37
	P	0.001	0.86	0.98	0.77	0.001	0.001	1.00	0.11	< 0.001
waterside	β	1.29	2.44	1.07	0.71	2.53	3.43	2.12	1.77	1.77
	SE	0.73	1.32	0.64	0.56	0.48	0.85	1.24	0.48	0.33
	Z	1.77	1.85	1.68	1.26	5.25	4.04	1.72	3.68	5.32
	P	0.31	0.47	0.37	0.62	< 0.001	< 0.001	0.28	< 0.001	< 0.001
temperature	β	0.09	0.08	0.08	-0.13	0.09	-0.01	-0.07	0.03	-0.04
	SE	0.05	0.09	0.05	0.04	0.03	0.08	0.07	0.04	0.00
	Z	2.03	0.84	1.67	-3.09	3.22	-0.08	-0.98	0.99	-8.83
	P	0.80	0.94	0.99	0.77	0.20	0.93	1.13	0.46	0.08
month08	β	0.80	0.94	0.99	0.77	0.20	0.93	1.13	0.46	0.08
	SE	0.49	0.95	0.50	0.67	0.30	0.96	0.85	0.39	0.32
	Z	1.64	0.99	1.98	1.15	0.66	0.97	1.32	1.20	0.25
	P	0.24	0.99	0.99	0.77	0.20	0.93	1.13	0.46	0.08
month09	β	-0.24	-0.67	-0.13	1.62	-0.54	-0.41	0.96	0.10	0.12
	SE	0.40	0.82	0.43	0.54	0.24	0.84	0.67	0.32	0.26
	Z	-0.61	-0.82	-0.31	2.99	-2.23	-0.49	1.45	0.32	0.45
	P	0.54	0.41	0.75	0.01	0.03	0.62	0.15	0.75	0.65
AIC		1007.7	396.0	723.6	1616.3	1717.3	758.2	671.6	1360.9	2212.1
full model										
AIC		1024.5	393.1	718.1	1641.7	1759.0	763.0	668.9	1361.0	2244.5
null model										
R2		0.376	0.131	0.122	0.361	0.466	0.193	0.183	0.134	0.367
marginal										
R2		0.571	0.132	0.379	0.715	0.579	0.551	0.566	0.368	0.458
conditional										

Temperature and months (month08 - August, month09 - September compared to July) were added as covariates into the models. The significant results are highlighted with bold characters. The P values were calculated by Dunnett's post-hoc tests controlling for multiple comparisons.

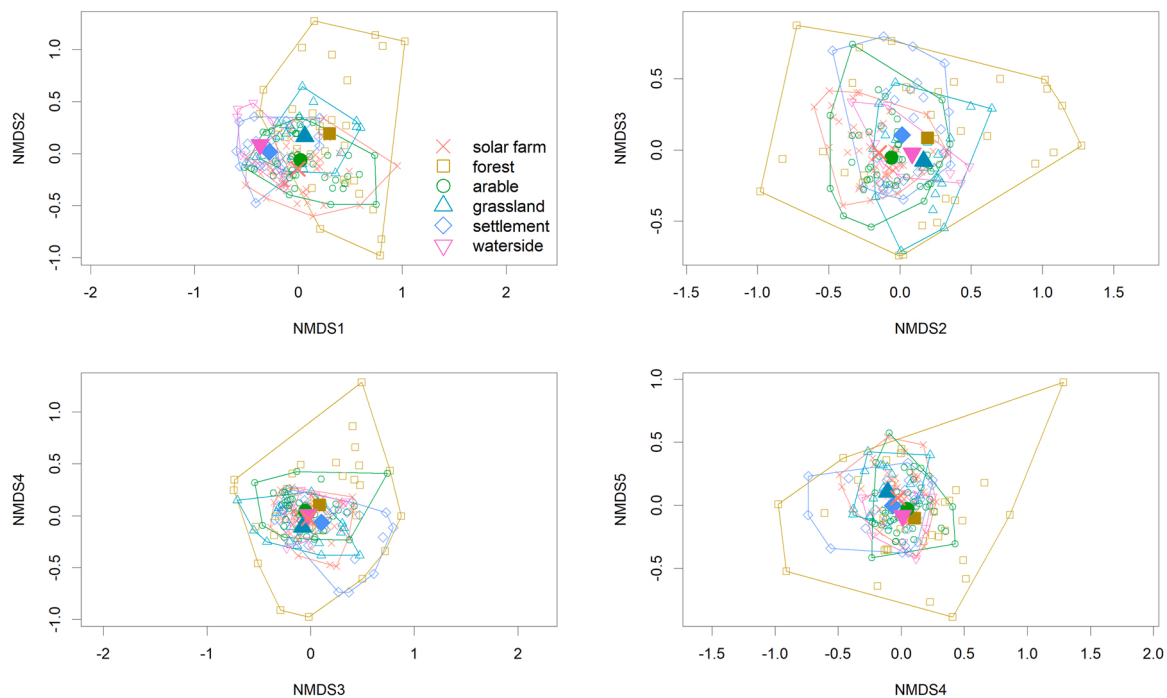


Fig. 4. The two-dimensional scatterplots of the non-metric multidimensional ordination analysis (stress value: 0.081). The graphs show the bat communities on 190 sampling points within six habitat types. The habitats are indicated with different colors and shape of points. The large symbols indicate the center of the convex hulls by habitats.

2016; Kusch and Schmitz, 2013; Rainho et al., 2010). Second, smooth artificial surfaces like solar panels have similar light polarization patterns to water, and these surfaces attract aquatic insects including Diptera, Ephemeroptera, Trichoptera, Odonata, Heteroptera and Coleoptera species (Horváth et al., 2011; Horváth et al., 2010; Horváth et al., 2009). These insects constitute a considerable part of the diets of several bat species including *N. noctula*, *P. kuhlii* and *P. nathusii* (Dietz and Kiefer, 2016) that were the most frequently detected species at the solar farms and feeding buzzes were also recorded from all of them. Here, we can only speculate that both sources of insects could contribute to the prey abundance at the solar farms and may have promoted the foraging of bats.

Bat species such as *H. savii*, *N. noctula*, *P. kuhlii* that thrive in urban landscapes (Ancillotto et al., 2015; Gili et al., 2020; Jung and Threlfall, 2016; Russo and Ancillotto, 2015; Zsebők et al., 2012) were also found in great abundance at solar farms indicating that selective pressure on the bat species may be similar to that in urbanized areas. While light and noise pollution are likely to be low at the solar farms, the extent of the smooth surfaces of solar panels may be larger than in the settlements. Our results suggest that solar farms may promote foraging habitats to species that are successfully adapted to anthropogenic environments. However, the most abundant species we found at the solar farms, such as *H. savii* and *P. kuhlii/nathusii*, were detected less often here compared to the surveyed green areas of settlements. This suggests that solar farms are less valuable for these species, perhaps due to the lack of suitable roosts and woody vegetation. It is important to note that we did not separate the echolocation calls of *P. kuhlii* and *P. nathusii* in statistical analyses because of the large overlap in their acoustic characteristics. However, social calls only from *P. kuhlii* were detected in solar farms and settlements and not from *P. nathusii*. Also, as previous studies showed that *P. kuhlii* is far more abundant in the urban areas than *P. nathusii* (Ancillotto et al., 2015; Zsebők et al., 2012), we can speculate that *P. kuhlii* is more abundant not only in urban areas but also in the solar farms than *P. nathusii*. Further investigations with larger sample sizes or other sampling techniques are needed to clarify this issue.

While some species like *H. savii*, *N. noctula* and *P. kuhlii* may be the winners of utilizing solar farms, other species may be the losers in this sense, a phenomenon described in other communities (Dornelas et al., 2019). Accordingly, we did not observe any activity of *B. barbastellus* - a species of major conservation concern - in solar farms and our model also revealed that the activity of *Myotis* spp. was significantly lower in solar farms than in forests and grasslands. We also found that the activity of *P. pygmaeus* tended to be lower at the solar farms compared to the grasslands. These findings indicate that while these species occur in cluttered, edge, and open habitats, solar farms may be suboptimal for them. *B. barbastellus* and several *Myotis* species are vulnerable and strictly protected in Hungary and throughout much of Europe (Dietz and Kiefer, 2016; Froidevaux et al., 2019; Mickleburgh et al., 2002), thus raising concerns about the placement and installation of solar farms within and close to valuable natural habitats. Additionally, we observed higher activity of *H. savii*, *N. noctula*, and *P. kuhlii* at solar farms than in forests; however, the primary foraging sites of these species are not in cluttered forests but mainly in open habitats (Dietz and Kiefer, 2016), and the dense vegetation in the forest may decrease the detectability of these species.

We found similar bat communities at solar farms and arable lands suggesting that these habitats provide similar ecological

Table A1
Summary of the sampling points by habitat and area.

Areas	Solar farm	Forest	Arable field	Grass-land	Settlement	Waterside	Σ
Bodony	3	3		2	3		11
Bogács	3	3	6				12
Bükkábrány	3	3	2	1	3		12
Csepel	6				6	1	13
Csepreg	5	5	5	5			20
Demjén	3	3	6				12
Felsőszolca	3		3		3		9
Hatvan	3		3		4		10
Kőszeg	5	5	5	5			20
Lőrinci	2		3		2		7
Sajóháony	3	2		3	3		11
Százhalombatta1	3				3	2	8
Százhalombatta2	4		5			4	13
Vép	5	5	5	5			20
Visonta	3	3	3			3	12
Σ	54	32	46	21	27	10	190

The number of sampling points are indicated in the cells. Altogether we sampled at 190 points, in 15 areas, and in 6 different habitats.

resources for some bat species (Wickramasinghe et al., 2003). Previously, the areas under intensive agriculture is found to be one of the poorest habitats for bats (Azam et al., 2016). Therefore, the results suggest that bat communities at solar farms are more similar to the “worst” habitat occurring the landscape, thus implying that solar farms are quite poor habitat too. Several studies suggested that the heterogeneity of agricultural habitats and the availability of linear features such as hedgerows can positively affect bat activity (Froidevaux et al., 2019; Monck-Whipp et al., 2018). Hence promoting the structuring of solar farms with hedgerows and tree lines for conservation purposes is likely to be beneficial for bat conservation. However, we have to note that many solar farms we sampled are surrounded by arable land that can also contribute to the similarities of the bat communities between these two habitat types.

Our study focused on the first four hours of the night, however, more detailed activity patterns can be revealed by long-term whole night sampling, especially using new features of Audiomoths such as frequency-based triggering that will reduce the numbers of recordings that need to be analyzed (Froidevaux et al., 2014). Multiple recording nights at each sampling point could also reveal clearer patterns as biotic and abiotic environmental stochasticity can then better be taken into account. It is also important to note that we sampled only in the summer and early autumn period of the year for practical reasons. However, the spring and the second half of the autumn could show different activity patterns of bats (Heim et al., 2016; Vasko et al., 2020) because of changes in prey availability (Jonason et al., 2014; Ruczyński et al., 2020), different migration patterns of the bat species (Krauel and McCracken, 2013) and the appearance of volant juvenile bats (Racey, 1982); further studies are therefore encouraged on seasonal changes in activity.

5. Conclusions

We found that bat species typically found in urbanized and agricultural habitats (*H. savii*, *N. noctula* and *P. kuhlii*) are often found at solar farms, while others (*Myotis* spp. and *B. barbastellus*) do not use solar farms frequently. As the number of solar farms is expected to proliferate globally in the near future, we need to understand the ecological role of solar farms in detail for future conservation actions. Further investigations are needed to reveal which insect groups are associated with the vegetation and attracted to solar panels at solar farms. It would be valuable to record the behavior (including foraging, orientation, drinking attempts, and collision) of bats and other vertebrates at solar farms in detail. Investigating the effects of size and heterogeneity of the solar farms, the location of the installations, the landscape context, and the cumulative impact of the solar farms in the landscape can significantly contribute to the development of conservation policy. We suggest a similar mitigation hierarchy as has been developed for wind farms (Peste et al., 2015). Accordingly, ecological impact assessments that take into account bats should be required before installing PV solar farms to avoid biodiversity loss; the installation of the solar farms should consider minimizing the diversity loss or even constructing diverse habitats; and for the already working solar farms, compensational acts should be taken. It is also important to reveal the differences in the use of solar farms by bats across different geographic regions to tailor the policy of management of PV solar farms to the local insect and vertebrate communities. Therefore, we suggest a global-scale monitoring at solar farms in a framework of international co-operation.

Funding

The project was supported by the Green Source “Zöld Forrás” grant (PTKF/327/2020).

CRedit authorship contribution statement

KLS, SZ – Conceptualization and Methodology; KLS, AK, SZ – Investigation; KLS, JSPF, SZ - Formal analysis; TG & PE – Supervision;

Table A2

Details of the sampled solar farms.

	Area	Longitude (WGS)	Latitude (WGS)	Angle of solar panels	Solar farm size (ha)	Month	Temp (°C)
1	Bodony	20.029	47.941	30	1.2	Sep	18.1 ± 2.2
2	Bogács	20.538	47.891	25	2.4	Aug	25.0 ± 1.7
3	Bükkábrány	20.705	47.893	33	20.0	Sep	24.6 ± 1.3
4	Csepel	19.035	47.393	10–30	0.8	Jul	22.0 ± 2.1
5	Csepreg	16.725	47.409	20	8.0	Jul	23.6 ± 2.7
6	Demjén	20.326	47.801	20	44.0	Aug	18.8 ± 2.2
7	Felsőszolca	20.893	48.122	35	45.0	Sep	21.2 ± 2.0
8	Hatvan	19.721	47.668	25	1.4	Sep	27.4 ± 2.0
9	Kőszeg	16.559	47.387	20	4.0	Jul	25.0 ± 2.3
10	Lőrinci	19.666	47.723	25	1.1	Sep	28.1 ± 0.8
11	Sajóbábony	20.709	48.158	25	2.2	Aug	23.2 ± 1.9
12	Százhalombatta1	18.925	47.323	20	7.4	Jul	28.0 ± 1.1
13	Százhalombatta2	18.905	47.332	20	23.0	Jul	28.1 ± 1.5
14	Vép	16.681	47.227	20	5.5	Jul	19.6 ± 3.7
15	Visonta	20.058	47.803	20	30.0	Sep	25.0 ± 2.0

The table contains the most important data about the solar farms studied: the settlements, coordinates, angle of solar panels, basic area, sampling month and temperature of the sampling night (mean ± SD).

draft writing – all authors.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We thank the operators and owners of the solar parks and Bükk and Órség National Park Directorates for their contribution to the survey. We also thank Gerhard Golen for his help during the fieldwork.

Appendix A

See appendix [Tables A1 and A2](#).

References

- Alvarez-Castañeda, S.T., Lidicker Jr., W.Z., 2015. Managing coexistence for bats and wind turbines. *Therya* 6, 505–513. <https://doi.org/10.12933/therya-15-330>.
- Ancillotto, L., Tomassini, A., Russo, D., 2015. The fancy city life: Kuhl's pipistrelle, *Pipistrellus kuhlii*, benefits from urbanisation. *Wildl. Res.* 42, 598–606. <https://doi.org/10.1071/WR15003>.
- Avila-Flores, R., Fenton, M.B., 2005. Use of spatial features by foraging insectivorous bats in a large urban landscape. *J. Mammal.* 86, 1193–1204. <https://doi.org/10.1644/04-MAMM-A-085R1.1>.
- Azam, C., Le Viol, I., Julien, J.F., Bas, Y., Kerbiriou, C., 2016. Disentangling the relative effect of light pollution, impervious surfaces and intensive agriculture on bat activity with a national-scale monitoring program. *Landsc. Ecol.* 31, 2471–2483. <https://doi.org/10.1007/s10980-016-0417-3>.
- Baerwald, E.F., D'Amours, G.H., Klug, B.J., Barclay, R.M.R., 2008. Barotrauma is a significant cause of bat fatalities at wind turbines. *Curr. Biol.* 18, 695–696. <https://doi.org/10.1016/j.cub.2008.06.029>.
- Báldi, A., Batáry, P., Kleijn, D., 2013. Effects of grazing and biogeographic regions on grassland biodiversity in Hungary – analysing assemblages of 1200 species. *Agric., Ecosyst. Environ.* 166, 28–34. <https://doi.org/10.1016/j.agee.2012.03.005>.
- Barré, K., Le Viol, I., Bas, Y., Julliard, R., Kerbiriou, C., 2018. Estimating habitat loss due to wind turbine avoidance by bats: implications for European siting guidance. *Biol. Conserv.* 226, 205–214. <https://doi.org/10.1016/j.biocon.2018.07.011>.
- Bartoń, K., 2020. MuMIn: Multi-model inference. R package version 1.43.17. Available from: <https://cran.r-project.org/web/packages/MuMIn/index.html> (accessed December 14, 2022).
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1), 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Bivand, R., 2020. spdep: Spatial Dependence: Weighting Schemes, Statistics. R package version 1.1–5. Available from: <https://cran.r-project.org/web/packages/spdep/index.html> (accessed December 14, 2022).
- Boldogh, S., Dobrosi, D., Samu, P., 2007. The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterologica* 9, 527–534. [https://doi.org/10.3161/1733-5329\(2007\)9\[527:TEOTTO\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2007)9[527:TEOTTO]2.0.CO;2).

- Bonari, G., Fajmon, K., Malenovsky, I., Zelený, D., Holuša, J., Jongepierová, I., Kočárek, P., Konvička, O., Uříčár, J., Chytrý, M., 2017. Management of semi-natural grasslands benefiting both plant and insect diversity: The importance of heterogeneity and tradition. *Agric., Ecosyst. Environ.* 246, 243–252. <https://doi.org/10.1016/j.agee.2017.06.010>.
- Browning, E., Barlow, K.E., Burns, F., Hawkins, C., Boughey, K., 2021. Drivers of European bat population change: a review reveals evidence gaps. *Mammal. Rev.* 51, 353–368. <https://doi.org/10.1111/mam.12239>.
- Carr, A., Weatherall, A., Jones, G., 2020. The effects of thinning management on bats and their insect prey in temperate broadleaved woodland. *For. Ecol. Manag.* 457, 117682. <https://doi.org/10.1016/j.foreco.2019.117682>.
- Chock, R.Y., Clucas, B., Peterson, E.K., Blackwell, B.F., Blumstein, D.T., Church, K., Fernández-Juricic, E., Francescoli, G., Greggor, A.L., Kemp, P., Pinho, G.M., Sanzenbacher, P.M., Schulte, B.A., Toni, P., 2021. Evaluating potential effects of solar power facilities on wildlife from an animal behavior perspective. *Conserv. Sci. Pract.* 3, 319–328. <https://doi.org/10.1111/csp2.319>.
- Ciechanowski, M., 2015. Habitat preferences of bats in anthropogenically altered, mosaic landscapes of northern Poland. *Eur. J. Wildl. Res.* 61, 415–428. <https://doi.org/10.1007/s10344-015-0911-y>.
- R. Core Team (2019): R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna. Available from: <https://www.R-project.org/> (accessed December 14, 2022).
- Cryan, P.M., Barclay, R.M.R., 2009. Causes of bat fatalities at wind turbines: hypotheses and predictions. *J. Mammal.* 90, 1330–1340. <https://doi.org/10.1644/09-MAMM-S-076R1.1>.
- Cryan, P.M., Gorresen, P.M., Hein, C.D., Schirmacher, M.R., Diehl, R.H., Huso, M.M., Hayman, D.T.S., Fricker, P.D., Bonaccorso, F.J., Johnson, D.H., Heist, K., Dalton, D.C., 2014. Behavior of bats at wind turbines. *Proceedings of the National Academy of Sciences of the United States of America* 111, 15126–15131. <https://doi.org/10.1073/pnas.1406672111>.
- Dahl, E.L., Bevanger, K., Nygård, T., Roskaft, E., Stokke, B.G., 2012. Reduced breeding success in white-tailed eagles at Smøla windfarm, western Norway, is caused by mortality and displacement. *Biol. Conserv.* 145, 79–85. <https://doi.org/10.1016/j.biocon.2011.10.012>.
- Dietz, C., Kiefer, A., 2016. *Bats of Britain and Europe*. Bloomsbury Publishing, London.
- Dornelas, M., Gotelli, N.J., Shimadzu, H., Moyes, F., Magurran, A.E., McGill, B.J., 2019. A balance of winners and losers in the Anthropocene. *Ecol. Lett.* 22, 847–854. <https://doi.org/10.1111/ele.13242>.
- Drewitt, A.L., Langston, R.H.W., 2006. Assessing the impacts of wind farms on birds: impacts of wind farms on birds. *Ibis* 148, 29–42. <https://doi.org/10.1111/j.1474-919X.2006.00516.x>.
- Duvergé, P.L., Jones, G., Rydell, J., Ransome, R.D., 2000. Functional significance of emergence timing in bats. *Ecography* 23, 32–40. <https://doi.org/10.1034/j.1600-0587.2000.230104.x>.
- Filgueiras, B.K.C., Peres, C.A., Melo, F.P.L., Leal, I.R., Tabarelli, M., 2021. Winner–loser species replacements in human-modified landscapes. *Trends Ecol. Evol.* 36, 545–555. <https://doi.org/10.1016/j.tree.2021.02.006>.
- Frey-Ehrenbold, A., Bontadina, F., Arlettaz, R., Obrist, M.K., 2013. Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *J. Appl. Ecol.* 50, 252–261. <https://doi.org/10.1111/1365-2664.12034>.
- Frick, W.F., Kingston, T., Flanders, J., 2019. A review of the major threats and challenges to global bat conservation. *Ann. N. Y. Acad. Sci.* 1469, 5–25. <https://doi.org/10.1111/nyas.14045>.
- Froidevaux, J.S.P., Zellweger, F., Bollmann, K., Obrist, M.K., 2014. Optimizing passive acoustic sampling of bats in forests. *Ecol. Evol.* 4, 4690–4700. <https://doi.org/10.1002/ece3.1296>.
- Froidevaux, J.S.P., Boughey, K.L., Hawkins, C.L., Broyles, M., Jones, G., 2019. Managing hedgerows for nocturnal wildlife: Do bats and their insect prey benefit from targeted agri-environment schemes? *J. Appl. Ecol.* 56, 1610–1623. <https://doi.org/10.1111/1365-2664.13412>.
- Gilli, F., Newson, S.E., Gillings, S., Chamberlain, D.E., Border, J.A., 2020. Bats in urbanising landscapes: habitat selection and recommendations for a sustainable future. *Biol. Conserv.* 241, 108343. <https://doi.org/10.1016/j.biocon.2019.108343>.
- Greif, S., Siemers, B.M., 2010. Innate recognition of water bodies in echolocating bats. *Nat. Commun.* 1, 107. <https://doi.org/10.1038/ncomms1110>.
- Greif, S., Zsebök, S., Schmieder, D., Siemers, B.M., 2017. Acoustic mirrors as sensory traps for bats. *Science* 357, 1045–1047. <https://doi.org/10.1126/science.aam7817>.
- Harrison, C., Lloyd, H., Field, C., 2017. Evidence review of the impact of solar farms on birds, bats and general ecology. Natural England Technical Report. Available from: <https://10.13140/RG.2.2.24726.96325> (accessed December 14, 2022).
- Hartig, F., 2021. DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.3. Available from: <https://cran.r-project.org/web/packages/DHARMA/index.html> (accessed December 14, 2022).
- Heim, O., Schröder, A., Eccard, J., Jung, K., Voigt, C.C., 2016. Seasonal activity patterns of European bats above intensively used farmland. *Agric., Ecosyst. Environ.* 233, 130–139. <https://doi.org/10.1016/j.agee.2016.09.002>.
- Hernandez, R.R., Easter, S.B., Murphy-Mariscal, M.L., Maestre, F.T., Tavassoli, M., Allen, E.B., Barrows, C.W., Belnap, J., Ochoa-Hueso, R., Ravi, S., Allen, M.F., 2014. Environmental impacts of utility-scale solar energy. *Renew. Sustain. Energy Rev.* 29, 766–779. <https://doi.org/10.1016/j.rser.2013.08.041>.
- Hill, A.P., Prince, P., Covarrubias, E.P., Doncaster, C.P., Snaddon, J.L., Rogers, A., 2018. AudioMoth: evaluation of a smart open acoustic device for monitoring biodiversity and the environment. *Methods Ecol. Evol.* 9, 1199–1211. <https://doi.org/10.1111/2041-210X.12955>.
- Horváth, G., Kriska, G., Malik, P., Robertson, B., 2009. Polarized light pollution: a new kind of ecological photopollution. *Front. Ecol. Environ.* 7, 317–325. <https://doi.org/10.1890/080129>.
- Horváth, G., Blahó, M., Egri, Á., Kriska, G., Seres, I., Robertson, B., 2010. Reducing the maladaptive attractiveness of solar panels to polarotactic insects. *Conserv. Biol.* 24, 1644–1653. <https://doi.org/10.1111/j.1523-1739.2010.01518.x>.
- Horváth, G., Móra, A., Bernáth, B., Kriska, G., 2011. Polarotaxis in non-biting midges: female chironomids are attracted to horizontally polarized light. *Physiol. Behav.* 104, 1010–1015. <https://doi.org/10.1016/j.physbeh.2011.06.022>.
- Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. *Biom. J.* 50, 346–363. <https://doi.org/10.1002/bimj.200810425>.
- Ingeme, Y., Bush, A., Lumsden, L., van Harten, E., Bourne, S., Reardon, T., 2018. Hit or miss could mean life or death for juvenile southern bent-wing bats. *Australasian Bat Society News* 50, 59. Available from: <http://st1.asflib.net/JNS/AUNat/ASF/ASF-ConfProc/ASFConfProcs31.htm> 1 (accessed December 14, 2022).
- Jaeger-Waldau, A., 2019. European Commission. Joint Research Centre. PV status report 2019. Available from: https://op.europa.eu/publication/manifestation_identifier/PUB_KJNA29938ENN (accessed December 14, 2022).
- Jonason, D., Franzén, M., Ranius, T., 2014. Surveying moths using light traps: effects of weather and time of year. *PLoS ONE* 9, e92453. <https://doi.org/10.1371/journal.pone.0092453>.
- Jung, K., Threlfall, C.G., 2016. Urbanisation and its effects on bats—A global meta-analysis. In: Voigt, C.C., Kingston, T. (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer International Publishing, Cham, pp. 13–33. https://doi.org/10.1007/978-3-319-25220-9_2.
- Krauel, J.J., McCracken, G.F., 2013. Recent Advances in Bat Migration Research. In: Adams, R.A., Pedersen, S.C. (Eds.), *Bat Evolution, Ecology, and Conservation*. Springer, New York, New York, NY, pp. 293–313. https://doi.org/10.1007/978-1-4614-7397-8_15.
- Kusch, J., Schmitz, A., 2013. Environmental factors affecting the differential use of foraging habitat by three sympatric species of *Pipistrellus*. *Acta Chiropterologica* 15, 57–67. <https://doi.org/10.3161/150811013X667858>.
- Lewis, S.L., Maslin, M.A., 2015. Defining the anthropocene. *Nature* 519, 171–180. <https://doi.org/10.1038/nature14258>.
- Mac Aodha, O., Gibb, R., Barlow, K.E., Browning, E., Firman, M., Freeman, R., Harder, B., Kinsey, L., Mead, G.R., Newson, S.E., Pandourski, I., Parsons, S., Russ, J., Szodoray-Paradi, A., Szodoray-Paradi, F., Tilova, E., Girolami, M., Brostow, G., Jones, K.E., 2018. Bat detective—Deep learning tools for bat acoustic signal detection. *PLoS Comput. Biol.* 14, 1–19. <https://doi.org/10.1371/journal.pcbi.1005995>.
- Mickleburgh, S.P., Hutson, A.M., Racey, P.A., 2002. A review of the global conservation status of bats. *Oryx* 36, 18–34. <https://doi.org/10.1017/S0030605302000054>.

- Monck-Whipp, L., Martin, A.E., Francis, C.M., Fahrig, L., 2018. Farmland heterogeneity benefits bats in agricultural landscapes. *Agric., Ecosyst. Environ.* 253, 131–139. <https://doi.org/10.1016/j.agee.2017.11.001>.
- Obrist, M.K., Boesch, R., Flückiger, P.F., 2004. Variability in echolocation call design of 26 Swiss bat species: consequences, limits and options for automated field identification with a synergetic pattern recognition approach. *Mammalia* 68, 307–322. <https://doi.org/10.1515/mamm.2004.030>.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Wagner, H., 2016. *vegan: Community ecology package*. R package version 2.4–1. Available from: <https://CRAN.R-project.org/package=vegan> (accessed December 14, 2022).
- Papadatou, E., Butlin, R.K., Altringham, J.D., 2008. Identification of bat species in Greece from their echolocation calls. *Acta Chiropterologica* 10, 127–143. <https://doi.org/10.3161/150811008X331153>.
- Peste, F., Paula, A., da Silva, L.P., Bernardino, J., Pereira, P., Mascarenhas, M., Costa, H., Vieira, J., Bastos, C., Fonseca, C., Pereira, M.J.R., 2015. How to mitigate impacts of wind farms on bats? A review of potential conservation measures in the European context. *Environ. Impact Assess. Rev.* 51, 10–22. <https://doi.org/10.1016/j.eiar.2014.11.001>.
- Pfalzer, G., Kusch, J., 2003. Structure and variability of bat social calls: implications for specificity and individual recognition. *J. Zool., Lond.* 261, 21–33. <https://doi.org/10.1017/S0952836903003935>.
- Racey, P.A., 1982. Ecology of Bat Reproduction. In: Kunz, T.H. (Ed.), *Ecology of Bats*. Springer, Boston, MA. https://doi.org/10.1007/978-1-4613-3421-7_2.
- Rainho, A., Augusto, A.M., Palmeirim, J.M., 2010. Influence of vegetation clutter on the capacity of ground foraging bats to capture prey: Vegetation clutter and ground foraging bats. *J. Appl. Ecol.* 47, 850–858. <https://doi.org/10.1111/j.1365-2664.2010.01820.x>.
- Ratcliffe, J.M., Elemans, C.P.H., Jakobsen, L., Surlykke, A., 2013. How the bat got its buzz, 20121031 *Biol. Lett.* 9. <https://doi.org/10.1098/rsbl.2012.1031>.
- REN21 Report, Renewables 2022 global status report; REN21 Secretariat. Available from: https://www.ren21.net/wp-content/uploads/2019/05/GSR2022_Full_Report.pdf (accessed December 14, 2022).
- Ruczyński, I., Hala, Z., Zegarek, M., Borowik, T., Dechmann, D.K., 2020. Camera transects as a method to monitor high temporal and spatial ephemerality of flying nocturnal insects. *Methods Ecol. Evol.* 11 (2), 294–302. <https://doi.org/10.1111/2041-210X.13339>.
- Russo, D., Ancillotto, L., 2015. Sensitivity of bats to urbanization: a review. *Mamm. Biol.* 80, 205–212. <https://doi.org/10.1016/j.mambio.2014.10.003>.
- Russo, D., Jones, G., 2002. Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. *J. Zool.* 258, 91–103. <https://doi.org/10.1017/S0952836902001231>.
- Russo, D., Jones, G., 2003. Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: conservation implications. *Ecography* 26, 197–209. <https://doi.org/10.1034/j.1600-0587.2003.03422.x>.
- Stone, E.L., Harris, S., Jones, G., 2015. Impacts of artificial lighting on bats: a review of challenges and solutions. *Mamm. Biol.* 80, 213–219. <https://doi.org/10.1016/j.mambio.2015.02.004>.
- Száz, D., Mihályi, D., Farkas, A., Egri, Á., Barta, A., Kriska, G., Robertson, B., Horváth, G., 2016. Polarized light pollution of matte solar panels: anti-reflective photovoltaics reduce polarized light pollution but benefit only some aquatic insects. *J. Insect Conserv.* 20, 663–675. <https://doi.org/10.1007/s10841-016-9897-3>.
- Vasko, V., Blomberg, A.S., Vesterinen, E.J., Suominen, K.M., Ruokolainen, L., Brommer, J.E., Norrdahl, K., Niemelä, P., Laine, V.N., Selonen, V., Santangeli, A., Lilley, T.M., 2020. Within-season changes in habitat use of forest-dwelling boreal bats. *Ecol. Evol.* 10, 4164–4174. <https://doi.org/10.1002/ece3.6253>.
- Voigt, C.C., Kingston, T., 2016. Bats in the Anthropocene. In: Voigt, C.C., Kingston, T. (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer International Publishing, Cham, pp. 1–9. https://doi.org/10.1007/978-3-319-25220-9_1.
- Voigt, C.C., Popa-Lisseanu, A.G., Niermann, I., Kramer-Schadt, S., 2012. The catchment area of wind farms for European bats: a plea for international regulations. *Biol. Conserv.* 153, 80–86. <https://doi.org/10.1016/j.biocon.2012.04.027>.
- Walters, C.L., Freeman, R., Collen, A., Dietz, C., Brock Fenton, M., Jones, G., Obrist, M.K., Puechmille, S.J., Sattler, T., Siemers, B.M., Parsons, S., Jones, K.E., 2012. A continental-scale tool for acoustic identification of European bats. *J. Appl. Ecol.* 49, 1064–1074. <https://doi.org/10.1111/j.1365-2664.2012.02182.x>.
- Waters, C.N., Zalasiewicz, J., Summerhayes, C., Barnosky, A.D., Poirier, C., Galuszka, A., Cearreta, A., Edgeworth, M., Ellis, E.C., Ellis, M., Jeandel, C., Leinfelder, R., McNeill, J.R., Richter, D. deB., Steffen, W., Syvitski, J., Vidas, D., Waprich, M., Williams, M., Zhisheng, A., Grinevald, J., Odada, E., Oreskes, N., Wolfe, A.P., 2016. The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science* 351, aad2622. <https://doi.org/10.1126/science.aad2622>.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York. ISBN 978-3-319-24277-4, Available from: <https://ggplot2.tidyverse.org>. (accessed December 14, 2022).
- Wickramasinghe, L.P., Harris, S., Jones, G., Vaughan, N., 2003. Bat activity and species richness on organic and conventional farms: impact of agricultural intensification. *J. Appl. Ecol.* 40, 984–993. <https://doi.org/10.1111/j.1365-2664.2003.00856.x>.
- Wieringa, J.G., Carstens, B.C., Gibbs, H.L., 2021. Predicting migration routes for three species of migratory bats using species distribution models. *PeerJ* 9, e11177. <https://doi.org/10.7717/peerj.11177>.
- Zsebök, S., Estók, P., Görföl, T., 2012. Acoustic discrimination of *Pipistrellus kuhlii* and *Pipistrellus nathusii* (Chiroptera: Vespertilionidae) and its application to assess changes in species distribution. *Acta Zool. Acad. Sci. Hung.* 58, 199–209.