



**HUNGARIAN UNIVERSITY OF
AGRICULTURE AND LIFE SCIENCES**

**ECOACOUSTIC STUDY OF ENVIRONMENTAL CHANGES
DRIVEN BY ANTHROPOGENIC IMPACTS ON BATS**

Thesis of PhD Dissertation

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BACKGROUND AND OBJECTIVES

Bats are the second most species-rich order of mammals, representing approximately one fifth of terrestrial wild mammal species and thus contributing substantially to global biodiversity (Greenspoon *et al.*, 2023; Simmons and Cirranello, 2023; Wilson and Mittermeier, 2019). Bats provide key ecosystem services in both agricultural and natural habitats, such as pollination, seed dispersal, and the regulation of arthropod populations (Kunz *et al.*, 2011). However, their populations show marked declines due to various human activities. Therefore, identifying the factors that threaten bats and developing bat-friendly practices to mitigate these negative impacts is of critical importance. This doctoral dissertation investigates the effects of different human-driven environmental changes on bats and summarizes the results of three studies.

During our research, we were among the first to examine the effects of one of the most rapidly expanding – solar farms – renewable energy sources on bats. As part of global efforts to mitigate climate change, the use of renewable energy has increased substantially worldwide. Over the past decade, the global extent of photovoltaic (PV) solar parks has expanded rapidly due to improvements in efficiency, decreasing hardware costs, and the possibility of feeding surplus electricity into the grid (Harrison *et al.*, 2017). Over the past decade, on- and off-grid solar capacity expanded from about 70 GW to 942 GW by 2021. (REN21 report, 2022). Given that producing of 1 MW of electricity requires between 1.5 and 3.5 hectares of land (Blaydes *et al.*, 2021; Walston *et al.*, 2021), high-demand regions such as Europe, Japan and India may need to allocate 0.5–5% of their total land area to solar parks by 2050 to cover their energy needs (Van De Ven *et al.*, 2021). Due to their large land requirements, the installation of solar power plants may conflict with agricultural land use and biodiversity conservation. In addition to potential loss of roosting and foraging habitat, photovoltaic solar parks—through the appearance of large smooth surfaces—may also pose challenges for bats during orientation. Although the specific effects of solar panels on bats are

not yet known, Greif and Siemers (2010) found that bats perceive horizontal, smooth surfaces (acoustic mirrors) as water because of their similar echo-acoustic properties.

Our second study tested, by combining three research methods, whether simple mechanical modifications can mitigate the negative, misleading effects of artificial smooth surfaces on bats. Human-driven alteration of the environment not only changes natural landscapes but also creates new challenges for wildlife. As a result of anthropogenic impacts, some organisms face sensory challenges. Animals rely on different sensory systems to process environmental information—such as hearing, smell, echolocation, the detection of electric and magnetic fields, and vibration—and disturbances to these systems can induce behavioural changes with individual-, population- and ecosystem-level consequences. Smooth surfaces represent a relatively understudied source of sensory disturbance; therefore, the increasing number of such surfaces (e.g., glass windows and solar panels) may cause serious problems for wildlife. One of the main causes of bird mortality is collision with glass buildings (Klem, 1990; Loss *et al.*, 2014; Santos, De Abreu and De Vasconcelos, 2017), while polarized light reflected from smooth artificial surfaces can trigger maladaptive reproductive behaviour in aquatic insects, such as laying eggs on the surface of solar panels (Malik *et al.*, 2008; Horváth *et al.*, 2009, 2010). Bats use the echoes to locate, recognize and classify objects or vegetation features, such as trees, leaves, flowers and water bodies (Yovel *et al.*, 2008). Artificial smooth surfaces have acoustic-mirror properties, meaning that they deflect bat ultrasound so that most of the echo does not return to the source (Greif and Siemers, 2010). Because the acoustic pattern of horizontally placed smooth surfaces resembles that of a natural water bodies. bats may attempt to drink from such surfaces regardless of the material, as shown both under laboratory conditions (Greif and Siemers, 2010) and in natural settings (Russo, Cistrone and Jones, 2012). Vertical smooth surfaces are perceived as open flight paths, which can cause collisions and potential injuries

(Greif *et al.*, 2017). With increasing urbanization, artificial smooth surfaces pose a growing threat to bats, as they are not restricted to urban environments but also appear in areas far from cities.

In our third study, we examined how different parameters of livestock farms (the species kept, herd size, distance from settlements) and the surrounding landscape composition affect bat activity. Livestock farming plays a substantial role in the economy and ecosystems of rural areas, and even in the health of humans and wildlife. However, livestock-production systems vary widely based on kept species and their husbandry conditions, including access to pastures or outdoor paddocks, drug use, land use, production intensity, integration with crop-production systems, and the type of products (Steinfeld *et al.*, 2006). Livestock farms represent unique habitats that combine characteristics of urban and agricultural areas, and may therefore be particularly interesting for bats. Elements such as buildings, roads and artificial lighting reflect features of urban environments, while farm buildings may provide potential roost sites for urbanized species. Insects attracted by livestock and their manure can constitute an important food source, whereas trees, rows of trees and hedgerows around farm buildings can provide resting sites, orientation cues and commuting routes for bats.

The overarching goal of our studies was to uncover the effects of different anthropogenic factors on bat behaviour and ecology.

In our first study we investigated the ecological impacts of solar parks on insectivorous bats. Using passive acoustic methods, our aims were:

- (i) to characterize the use of solar parks by bats,
- (ii) to compare species composition, frequency of occurrence and foraging activity between solar parks and other nearby habitats—forests, grasslands, arable fields, settlements and watersides—in mosaic landscapes.

The objectives of the second study included:

- (i) to test in practice the effects of mechanically modifying smooth surfaces on bat behaviour.
- (ii) We examined the sound-reflecting properties of modified surfaces using a playback experiment and
- (iii) mathematical modelling.

Our study focused on bats' perception of water and the associated drinking behaviour, as this can be studied with minimal disturbance and without the risk of injury compared to monitoring collision events.

In our third study, our aims were:

- (i) to describe the community composition of bats at livestock farms,
- (ii) to test the effects of farm characteristics (e.g., the species kept and herd size) and the composition of the surrounding landscape on bat activity,
- (iii) to compare bat activity between livestock farms and other habitats, taking landscape context into account.

MATERIALS AND METHODS

Investigation of the ecological impacts of solar parks on bats

We conducted the study at 15 sampling sites in Hungary in a mosaic landscape. We examined solar parks of different sizes (1.2–45 ha), where panel tilt angles ranged from 0 to 35 degrees. Each sampling site contained one solar park and a set of different control habitats located within a 5 km radius of the solar park, comprising forests, agricultural areas, grasslands, settlements and watersides. At each site, we designated 1–6 sampling points in each habitat type (mean 3.6 ± 1.3), depending on habitat size. In total, we collected data from 190 sampling points.

Acoustic sampling was carried out between 5 July and 16 September 2020. At each site we sampled only once, simultaneously at all sampling points within the site. Recordings started at sunset and lasted for 4 hours. Bat calls were restringed with AudioMoth (OpenAcousticDevices; Hill *et al.*, 2018; v1.1.0) full-spectrum detectors. Call sequences were identified manually to species or species-group level in Kaleidoscope Pro (Wildlife Acoustics, Inc.). Bat activity was quantified by summing the call sequences restringed during the night; this was calculated separately for each sampling point at the level of species and species groups, and we also calculated total bat activity irrespective of species.

To compare bat activity in solar parks and other habitats, we used generalized linear mixed models (GLMMs). To explore community-level habitat use, we applied non-metric multidimensional scaling (NMDS) using the ‘vegan’ package (Oksanen *et al.*, 2016).

Mitigation options for the deceptive effect of smooth surfaces

The field experiments were conducted in Budapest, in the botanical garden of Eötvös Loránd University, at a small artificial pond. On one side of the pond, we designated a 1×2 m area where we presented the different treatments to bats. The first treatment was the control, i.e., the water surface without any artificial object ($N = 6$ nights). The second treatment was a smooth black plastic plate (1×2 m) placed directly above the water surface without a gap ($N = 5$ nights). In the additional treatments, we attached black plastic strings to the top of the sheet, the strings were arranged parallel to the short side of the sheet, 20 cm apart. String diameters were 0.25, 0.50, 1.00, 1.50 and 2.50 mm ($N = 3, 5, 3, 3, 3$ sampling nights). Finally, we applied an additional treatment in which we placed four crosswise strings (diameter 0.50 mm) in addition to the nine parallel strands (diameter 0.50 mm) ($N = 5$ nights). In total, we used eight different treatments, applied in random order each night to eliminate the possibility that bats would habituate to a given treatment. Data collection took place from late July 2020 to early October. Experiments were carried out every other evening—on a total of 33 sampling nights—thereby providing undisturbed nights between experiments for the bats. Observations started at sunset and lasted approximately 90 minutes.

Bat behaviour above the presented smooth surfaces was restringed in night mode with two normal-speed cameras (from different angles). Infrared light was used to illuminate the area of interest. We also made audio restringings using an AudioMoth detector to determine species-specific bat activity. Video recordings were analysed using BORIS (Behavioural Observation Research Interactive Software; Friard and Gamba, 2016). We defined three behavioural events: ‘bat pass’, ‘drinking’, and ‘collision’. For each night, we summed the number of events per category and calculated the relative occurrence of drinking as the ratio of the number of ‘drinking’ events to the total number of ‘bat pass’ events. We used Kaleidoscope Pro (Wildlife Acoustics) to automatically identify bat calls to species, and then manually verified species identification following Russ (2012).

The effects of the smooth plate and the string-covered treatments on bat drinking behaviour were analysed using multiple statistical approaches. The effect of the smooth plate alone was analysed with a linear model (lm, R 4.1.0). The effect of placing the thinnest strings (0.25 mm) on the smooth surface relative to the smooth plate was assessed with a Wilcoxon rank-sum test. The relationship between drinking ratio and string diameter was examined with non-linear regression (drm, 'drc' package). We also tested the effect of string arrangement (parallel vs crossed; 0.5 mm strings) using a Wilcoxon test. All statistical calculations were performed in R, and figures were created using the ggplot2 package.

For the playback experiment, we created artificial echolocation pulses in R using the 'seewave' package. These were played back with an ultrasonic loudspeaker, and the returning echoes were restringed with an ultrasonic detector (Pettersson D1000X, Pettersson Elektronik AB, Uppsala, Sweden).

For each echo sequence, we generated spectrograms using the 'seewave' package, and then calculated the mean spectrogram and then extracted the spectrograms that exclusively displayed the echoes of the strings.

To examine the echoes of the strings and the smooth plate separately, and to analyse the effect of string diameter on echo strength, we developed a numerical simulation framework in MATLAB 2022b. We considered two configurations, calculating echo strength for (1) a string without a sheet and (2) a string attached to a smooth surface. The framework enabled estimation of reflected wave intensities by numerically solving the acoustic wave equation. Individual echo strengths were calculated up to second-order reflections using Kuttruff's (2017) acoustic mirror source method. The MATLAB code for the simulations can be requested at firtha@hit.bme.hu.

Effects of livestock farm characteristics and landscape composition on bat activity

We conducted acoustic sampling between 3 June and 30 August 2020 (using AudioMoth detectors) in Vas County, Hungary. Recordings started at sunset and lasted 4 hours at each sampling point; each point was sampled once. In total, we collected data from 199 sampling points across different habitat types. 92 sampling points were located at 35 livestock farms. At each farm, we deployed 1–5 detectors (2.6 ± 1.0) at varying distances within 50 m of livestock buildings (12.0 ± 12.7 m). We sampled cattle farms ($N = 20$), horse farms ($N = 7$), and mixed-stock farms—where, in addition to cattle or horses, other animals such as Hungarian grey, donkeys, bison, sheep, pigs and chickens were present ($N = 8$). Herd sizes ranged from 4–60 horses (18.3 ± 19.3), 10–1000 cattle (262.5 ± 306.5), and 15–522 individuals at mixed farms (138.4 ± 168.5). Farms were located at varying distances from the edge of the nearest settlement, between 0 and 1860 m (350 ± 470 m).

To describe landscape composition, we performed the following steps. We used the Ecosystem Map of Hungary (Tanács *et al.*, 2022) as a reference database and processed spatial data in QGIS 3.32.3 (Lima) (QGIS Development Team, 2009). We then quantified the relative frequency of six habitat types—agricultural land, artificial environment, coniferous forest, deciduous forest, grassland, and green areas within the artificial environment—within circular buffers of 100, 250, 500, 1000, 2000 and 3000 m radius around sampling points. A landscape cell was assigned to a given habitat type if that habitat dominated the 20 m grid cell.

In addition to livestock farms, we carried out acoustic sampling in six further habitat types to compare bat activity with that observed on farms. The ‘control’ habitats included arable fields ($N = 12$), grasslands ($N = 15$), oak ($N = 25$) and pine forests ($N = 17$), settlement roads ($N = 16$) and urban green areas ($N = 22$).

Restrained bat-call sequences were analysed automatically using SonoChiro (Biotope Society, France) and then checked manually.

All statistical analyses were performed in R, and plots were created using the 'ggplot2' package. Bat species occurring on livestock farms, species-specific and total activity, and feeding buzzes were analysed using GLMMs and GLMs, taking into account farm characteristics (livestock species, herd size) and the relative frequency of surrounding habitats. Model diagnostics were performed using the 'DHARMA' package (Hartig, 2022); residual distributions were evaluated using the 'performance' package (Lüdtke *et al.*, 2021); and spatial autocorrelation was tested by calculating Moran's I using the 'ape' package (Paradis and Schliep, 2019).

To compare the number of bat call sequences among species (based on 35 farms and a total of 92 sampling points), we fitted generalized linear mixed models with negative binomial error distribution to account for overdispersion.

To quantify within-farm variance, we fitted two GLMMs to test the effect of placement on total sequences. As we found no significant differences in bat activity between near and far locations, we excluded the proximity factor from subsequent statistical models. Instead, we randomly selected one sampling point per farm and used the activity values from these individual points for later analyses.

For objective (ii) (comparisons among livestock farms), we considered spatial scales with radii of 100, 250, 500, 1000, 2000 and 3000 m to cover the local environment where bats likely move nightly between roosts and foraging areas (Laforge *et al.*, 2021). For objective (iii) (habitat comparisons), however, we considered only the 1000, 2000 and 3000 m scales because the relative frequency of surrounding habitats was strongly correlated with the sampled habitats at scales smaller than 1000 m radius. To identify the best effect scale, for each habitat type we entered the relative frequency at different scales into the models one at a time and selected the scale at which the model best explained the

data based on AICc, calculated using the ‘dredge’ function of the ‘MuMIn’ package (Bartoń, 2010). We then included, in each linear model, the relative frequency of the six surrounding habitats (agricultural land, coniferous forest, deciduous forest, grassland, artificial environment, and green areas within the artificial environment).

To examine the effects of farm characteristics and surrounding habitats (objective ii), we built GLMs for individual bat species as well as for total bat activity and feeding buzzes.

To address objective (iii), we compared bat activity between livestock farms and control habitats. Here as well, we built GLMs separately for the number of call sequences of each focal species, for total bat-call sequences, and for feeding buzzes.

RESULTS AND DISCUSSION

Investigation of the ecological impacts of solar parks on bats

We recorded a total of 29,853 bat calls. Based on these, we identified six species and three species groups, as well as feeding buzzes. The fewest sequences were registered for *B. barbastellus*, which occurred mainly in forests, but was also detected in arable and grassland habitats. All other species and species groups were detected in all habitat types. Calls belonging to the *P. kuhlii/nathusii* group were restringed in the highest numbers (11,835 sequences), followed by *N. noctula* (6,906 sequences). In total, we restringed 197 feeding buzzes.

In solar parks, we detected all species and species groups except *B. barbastellus*. *P. kuhlii/nathusii* and *N. noctula* occurred at more than 98% of the sampling points in solar parks. Calls belonging to the QCF group, as well as *H. savii* and *N. leisleri*, were also present at more than 50% of the sampling points in this habitat type. We also detected feeding buzzes from different taxa in solar parks: 14 for *P. kuhlii/nathusii*, 10 for *N. noctula*, two for *H. savii* and the QCF group, and one for *P. pygmaeus*.

The number of detected sequences showed significant differences between solar parks and other habitat types for several bat taxa. Compared with solar parks, activity of *H. savii*, *P. kuhlii/nathusii* and *N. noctula* was significantly lower in forests, whereas activity of *Myotis* spp. was significantly higher. For *Myotis* spp. we also found significantly higher activity, and for *P. pygmaeus* a trend toward higher activity, in grasslands relative to solar parks. In settlements, activity of *H. savii*, *P. kuhlii/nathusii*, *P. pipistrellus* and overall bat activity were significantly higher than in solar parks. In waterside habitats, we restringed significantly more sequences than in solar parks for *P. kuhlii/nathusii*, *P. pipistrellus*, the QCF group, and overall bat activity. We found no significant differences in bat activity between arable fields and solar parks.

To further investigate the *P. kuhlii/nathusii* group, we also examined manually analysed social calls. We detected *P. kuhlii* social calls at two solar parks, two waterside sites, two grassland sites and three settlements, whereas *P. nathusii* social calls were detected at two waterside and one arable habitat, but not in solar parks.

Visual inspection of the NMDS results indicated substantial overlap in the distribution of sampling points of bat communities across the different habitat types. Bat communities of solar parks and agricultural habitats were the most similar, as the centroids of their point clouds were closest and their overlap was greatest in NMDS space.

Mitigation options for the deceptive effect of smooth surfaces

Field experiment

Across the 33 sampling nights, we registered a total of 6,691 bat passes and 688 drinking events. Above the experimental area, we observed passes and drinking behaviour only from small-sized bats. From the recordings we identified 1,002 echolocation call sequences belonging to small-sized bats. Of these, 846

(84.4%) were from *P. kuhlii*, 119 (11.9%) from *H. savii*, and 37 (3.7%) from *P. pipistrellus*.

We did not observe bats colliding with or landing on the plate. Over open water, bats showed drinking behaviour in 32% of passes (median), which decreased to 21% above the smooth plate without strings; however, this difference was not statistically significant (LM, $t = -1.93$, $F_{1,9} = 3.73$, $P = 0.085$). In case of plate with 0.25 mm strings, the proportion of drinking events was significantly lower than for the smooth plate without strings (one-sided Wilcoxon rank-sum test, $W = 15$, $P = 0.018$).

We found the drinking ratio to be significantly lower for the crossed string arrangement than for the parallel arrangement (one-sided Wilcoxon rank-sum test, $W = 22$, $P\text{-value} = 0.022$). No drinking attempts were observed under the crossed string arrangement.

For smooth sheets equipped with parallel strings, we found a decreasing trend in the proportion of drinking events with increasing string diameter. At a string diameter of 2.5 mm, no drinking events were recorded. Based on the results of the exponential decay model, the proportion of drinking events decreased significantly with increasing string diameter compared to the smooth-sheet treatment.

Playback experiment

Results of the playback experiment supported our hypothesis that echo strength is dependent of string diameter; thus, larger-diameter strings generate stronger echoes. Consequently, the thinnest strings (0.25 mm) produced much weaker echoes than the thickest strings (2.50 mm). In addition, increasing the number of strings produced stronger echoes, and as string diameter increased, echoes contained relatively stronger components in the low-frequency range. In regard to the smooth plate, we observed only the direct sound from the loudspeaker and the sound reflected perpendicularly from the sheet.

Analytical results

The mathematical calculations revealed clear trends in echo strength as a function of incoming sound frequency and string diameter. As expected, the strength of the reflected sound increased with both increasing diameter and increasing frequency. This trend was particularly clear in the lower frequency range up to 30 kHz for all diameters, and above 30 kHz up to a diameter of 0.5 mm. However, above 30 kHz, for strings with diameters of 1–5 mm, the strength of the reflected sound showed a decreasing trend. For 1 mm strings, intensity began to decrease above 90 kHz, whereas strings with diameters of 2.50 and 5 mm reflected sound with high variability.

The strength of the perpendicular echo from the smooth plate showed only a slight decrease with increasing frequency in the examined range, and was approximately 15 dB higher than the strongest string echo. Reflected sound strength was about 10 dB higher when the strings were placed on the smooth surface than when they were presented alone without a smooth surface.

Effects of livestock farm characteristics and landscape composition on bat activity

In total, we detected 28,412 bat-call sequences, of which 44.8% (12,722 sequences) could be identified using SonoChiro. The most common bat taxa at livestock farms were *Nyctalus* spp., *P. kuhlii/nathusii*, *P. pipistrellus* and *P. pygmaeus*, occurring at more than 68% of the surveyed farms. These taxa also yielded the highest numbers of call sequences, in some cases with more than 100 detections, and occasionally more than 1,000 sequences for *P. pygmaeus*. The number of bat-call sequences differed significantly among species; *B. barbastellus*, *H. savii* and *Myotis* spp. occurred less frequently on livestock farms and showed lower activity. Manual analysis of detected social calls found 208 sequences belonging to *P. kuhlii* from 13 different farms, and one detection of *P. nathusii* from one farm.

Placement of detectors within farms (near vs far from buildings) had no effect on the total number of bat-call sequences ($\beta = -0.40 \pm 0.31$, $z = -1.30$, $p = 0.13$, $N = 16$) or on the number of feeding buzzes ($\beta = -0.26 \pm 0.68$, $z = -0.38$, $p = 0.70$, $N = 16$). In some farms, however, we registered more feeding buzzes near buildings, with 10, 16 and 65 detections at cattle farms, and single detections at two other mixed-stock farms. All feeding buzzes detected farther from buildings were registered at cattle farms.

When comparing livestock farms, we found that both farm characteristics and landscape composition influenced bat activity. Livestock type had a significant effect on *P. kuhlii/nathusii* activity. Their activity was significantly higher at cattle farms than at horse farms. We found a significant positive relationship between *Nyctalus* spp. activity and the proportion of surrounding agricultural land as well as the proportion of artificial environment (within 250 m). In addition, we found a positive association between total bat activity and the proportion of green areas within the artificial environment (within 250 m).

When comparing bat activity between livestock farms and other habitats, we observed significant differences for *B. barbastellus*, *Nyctalus* spp., *Myotis* spp., *P. kuhlii/nathusii*, *P. pygmaeus* and total bat activity. Overall bat activity was significantly higher in livestock farms than in control habitats, excluding settlement habitats. Post-hoc tests indicated that activity of *Nyctalus* spp. was significantly higher at livestock farms compared with agricultural areas, grasslands, oak forests and green area in settlement. For the *P. kuhlii/nathusii* group, activity was higher at livestock farms compared with arable fields, both forest types and urban green areas, while for *P. pygmaeus*, activity was higher compared with arable fields. However, for *B. barbastellus* and *Myotis* spp., activity was lower at livestock farms than in oak forests. Furthermore, for *B. barbastellus* we observed higher activity in pine forests than at livestock farms.

CONCLUSIONS AND RECOMMENDATIONS

Investigation of the ecological impacts of solar parks on bats

In our research, we were among the first to investigate the effects of one of the most rapidly spreading renewable energy sources—solar parks—on bats using acoustic methods. Initially, we assumed that these habitats would be unfavourable for bats because they are often located in homogeneous agricultural landscapes and the smooth surface of solar panels can function as an acoustic mirror (Greif and Siemers, 2010; Greif *et al.*, 2017). In contrast, we observed substantial bat activity for several taxa, suggesting that orientation near solar panels is not a major obstacle. One possible explanation is that the metal structures supporting the panels provide sufficient acoustic cues. This is supported by the fact that, in solar parks, we recorded frequent occurrences of *Pipistrellus* species—typically associated with cluttered habitats—alongside higher-flying *Nyctalus* species and the QCF group.

Feeding buzzes detected within solar parks demonstrated that bats do not merely fly through these habitats but also can forage there. For solar parks, we propose several mechanisms that may contribute to the presence of insect prey. First, the solar parks we sampled generally had some low herbaceous understory vegetation, which can provide suitable habitat for various flying insect taxa such as *Hymenoptera*, *Lepidoptera*, *Diptera* and *Orthoptera* (Báldi *et al.*, 2013; Bonari *et al.*, 2017), which in turn can serve as prey for bats (Dietz and Kiefer, 2016; Kusch and Schmitz, 2013; Rainho *et al.*, 2010). Furthermore, the polarization pattern of light on certain types of solar panels may attract water-associated insects, including some dipterans (*Diptera*), beetles (*Coleoptera*) and true bugs (*Heteroptera*), as well as mayflies (*Ephemeroptera*), caddisflies (*Trichoptera*) and dragonflies (*Odonata*) (Horváth *et al.*, 2011; Horváth *et al.*, 2010; Horváth *et al.*, 2009). These insects comprise a substantial part of the diet of several bat species, including *N. noctula*, *P. kuhlii* and *P. nathusii* (Dietz and Kiefer, 2016), which

were the most frequently detected species in solar parks and for which we registered feeding buzzes as well. Because we did not assess insect availability during the study, we can only assume that both insect sources may have contributed to prey availability in solar parks and facilitated bat foraging.

As expected, bat species well adapted to urban environments, such as *H. savii*, *P. kuhlii* and *N. noctula* (Ancillotto *et al.*, 2015; Gili *et al.*, 2020; Jung and Threlfall, 2016; Russo and Ancillotto, 2015; Zsebök *et al.*, 2012), occurred in high numbers in solar parks, suggesting that these habitats may impose selection pressures on bat communities similar to those in urban areas. Although light and noise pollution are presumably lower, the presence of extensive smooth surfaces may fulfill functions similar to those in settlements. At the same time, activity of the most frequently detected taxa in solar parks (*H. savii* and *P. kuhlii/nathusii*) was lower than in settlements, indicating that solar parks are less optimal for them. This may be due to low habitat diversity and the lack of suitable roosts and woody vegetation. In solar parks and settlements, we detected social calls only from *P. kuhlii*. Given that previous studies indicate *P. kuhlii* is much more common in urban habitats, it is likely that it is also more dominant in solar parks, which should be confirmed by further targeted studies.

Different species adapt to novel habitats in different ways, in case of solar parks, some species—such as *H. savii*, *N. noctula* and *P. kuhlii*—may be able to exploit opportunities offered by solar parks, whereas other species may be disadvantaged. For example, we did not observe the *B. barbastellus* —a species of high conservation importance—in solar parks, and our model also showed that *Myotis* activity was significantly lower in solar parks than in forests and grasslands. *P. pygmaeus* activity was also lower in solar parks compared with grasslands. These results suggest that although these species occur in cluttered, edge and open habitats, solar parks may be suboptimal for them, therefore, installing solar power plants within or near valuable natural habitats raises a number of concerns.

Bat communities of solar parks most closely resembled those of arable fields, suggesting that these habitats provide similar ecological resources. It is important to note that the studied solar parks were often surrounded by arable land, which may contribute to the similarity between the two habitat types. Previous research indicates that areas under intensive agricultural management are among the least suitable habitats for bats (Azam *et al.*, 2016); accordingly, our results suggest that bat communities in solar parks may also resemble the ‘worst’ habitats in the landscape and can be considered rather impoverished. Nevertheless, as in agricultural habitats, structurally enriching the surroundings of solar parks (e.g., shrubs, tree rows) may benefit bats. In areas of low naturalness, solar parks designed according to conservation principles and managed extensively—for example, sites sown with native seed mixtures and maintained by one or two annual mowings or grazing, while avoiding herbicide use—may even increase ecological value by ensuring the long-term persistence of grasslands around the panels throughout the operational lifetime of the park (Tölgyesi *et al.*, 2023).

Our study was limited to the first four hours of the night and to the summer–early autumn period; however, all-night and multi-night sampling, as well as the inclusion of the spring and late autumn periods, could reveal more detailed and different activity patterns due to seasonal variation in prey dynamics and bat migration.

Because the number of solar parks will increase worldwide, it is important to explore the ecological role of these habitats in detail. Further research is needed on insect groups associated with solar panels and park vegetation, as well as on the behaviour of bats and other vertebrates (e.g., foraging, orientation, drinking attempts, collisions). Studying the size, heterogeneity, landscape setting and cumulative effects of solar parks could contribute substantially to the planning of conservation management. We recommend developing mitigation hierarchies similar to those established for wind turbines (Peste *et al.*, 2015). Accordingly,

photovoltaic solar parks also require pre-construction ecological impact assessments that explicitly consider bats. To avoid biodiversity loss, solar-park siting and installation should aim to minimize diversity loss, or even to create diverse habitats during construction; and for already operating solar parks, compensatory measures should be implemented. To uncover regional differences, we recommend coordinated global monitoring of solar parks within international collaborations.

Mitigation options for the deceptive effect of smooth surfaces

Our results showed that the number of bat's drinking attempts on artificial smooth surfaces can be reduced by placing long, straight, cylindrical objects (e.g., thin strings) on the smooth surface. Increasing string diameter enhanced the mitigation effect, which was supported by both the playback experiment and the mathematical modelling. We also found empirical evidence that using a crossed pattern, while maintaining the same spacing as the parallel arrangement, increases the mitigation effect.

In both the playback experiment and the mathematical modelling, using larger-diameter strings resulted in a marked increase in reflected-sound strength. Consistent with this, in the behavioural experiment the drinking ratio showed a nonlinear decreasing trend as diameter increased.

A previous study on the big brown bat (*Eptesicus fuscus*), which emits echolocation calls with peak energy between 35 and 45 kHz, also reported a nonlinear relationship between bat behaviour and the vertical arrangement of strings, with the largest behavioural change observed at a string diameter of 0.5 mm (Sümer, Denzinger and Schnitzler, 2009). Similarly to our findings, Greenfeld *et al.* (2018) showed that horizontally arranged strings with a diameter of 2 mm are readily detectable by *P. kuhlii*. Our results further suggest that bats are able to detect even small-diameter (≥ 0.25 mm) strings on smooth surfaces, which substantially reduces drinking behaviour.

Results from the playback experiment and the mathematical modelling both indicated that echo strength depends on sound frequency. In general, for sounds emitted between 10 and 150 kHz we observed an increase of approximately 5–10 dB in echo strength, which can be explained by the shorter wavelength of the signal at higher frequencies leading to greater reflection (Morse and Ingard, 1986; Pye, 1993; Houston, Boonman and Jones, 2004). However, above a string diameter of 0.5 mm, interference phenomena cause strong fluctuations in echo intensity, which appear as an apparent decrease in intensity (Morse and Ingard, 1986; Pye, 1993). Consequently, these results suggest that further increasing string diameter—especially above 1 mm—contributes to stronger echo formation mainly in the low-frequency range. In mitigation measures targeting bats, this phenomenon must be considered, ensuring that string diameter is well matched to the wavelengths of the calls emitted by the target species.

Mathematical calculations showed that strings placed on a smooth surface produced echoes approximately 10 dB stronger than strings presented without a surface. This can be explained by the fact that not only the echo from the string itself, but also reflections formed between the string and the surface, increase echo strength. Because the acoustic-mirror effect may facilitate detection of strings placed on smooth surfaces, it is advisable to exploit this phenomenon when designing future mitigation approaches.

String arrangement may influence the mitigation effect, because bats approach the area from different directions and the strongest echo back towards the sound source is expected when the sound hits the strings perpendicularly. Consistent with this, we observed a statistically lower drinking ratio for the crossed string arrangement. Therefore, future mitigation methods should consider using cylindrical objects with good sound-reflecting properties arranged in multiple directions.

In our study, the smooth plastic plate reproduced the water surface well acoustically, as indicated by the fact that bats' drinking behaviour did not differ significantly between the two surfaces. Because the acoustic-mirror phenomenon is independent of material (Greif and Siemers, 2010), any human-made smooth surface may cause orientation problems. From a practical perspective, it is crucial to determine which surfaces can be considered acoustic mirrors. At the same time, the acoustic properties of surfaces may vary with their roughness, which can be substantial in anthropogenic environments due to manufacturing differences. This highlights the need for further research aimed at quantitative characterization of surface roughness and acoustic properties. In this context, we propose a three-step mitigation plan: first, identify potentially problematic smooth surfaces; second, apply objects suitable for mitigation on these surfaces; and finally, monitor the modified surfaces to observe changes in bat behaviour.

Potentially, any large smooth surface—such as windows, solar panels, or plastic and metal surfaces—at different tilt angles can disrupt bat navigation, but modifying every object is practically impossible. Because bats show a strong innate recognition of water, they may repeatedly attempt to drink from horizontal smooth surfaces. Under natural conditions, however, most individuals abandon such sites and search for alternative drinking locations within a short time (Greif and Siemers, 2010; Russo, Cistrone and Jones, 2012). This behaviour may become energetically costly when artificial smooth surfaces are more abundant than natural water bodies, a situation that is likely to occur in dry or heavily modified landscapes, such as desert solar power plants.

Proximity of smooth surfaces to bat colonies, hibernation sites or migration routes may increase collision risk, especially for juveniles that lack experience in avoiding such surfaces (Ingeme *et al.*, 2018). Artificial smooth surfaces that are close to horizontal, especially in dry environments, may hinder the detection of water bodies. Therefore, applying mitigation techniques is particularly important for smooth surfaces occurring in such areas.

Our results indicate that thin, linear objects spaced relatively far apart (20 cm) can be effective in mitigating acoustic pollution. Such linear structures occupy only a small proportion of the surface, allowing for the development of mitigation solutions that minimally affect visibility through windows or the energy production of solar panels. In addition, light-coloured or high-contrast patterns may provide further benefits by reducing attraction caused by polarized light, thereby serving as cues for multiple animal taxa simultaneously.

In summary, our study presents an effective and easily applicable method to mitigate the impacts of smooth surfaces, supported by behavioural experiments, playback, and mathematical modelling. However, further research is needed to clarify the sensory and behavioural mechanisms involved and to assess the ecological and fitness consequences of smooth surfaces, especially in large-scale artificial environments such as solar parks (Barré *et al.*, 2023; Szabadi *et al.*, 2023; Tinsley *et al.*, 2023).

Effects of livestock farm characteristics and landscape composition on bat activity

In our study, we detected four bat species and three species groups at the surveyed livestock farms. We found relationships between the activity of certain bat species, farm characteristics and landscape composition. In addition, we observed that the activity of several bat taxa was higher at livestock farms than in other habitats.

The most frequently detected taxa—*Nyctalus* spp., *P. kuhlii/nathusii*, *P. pipistrellus* and *P. pygmaeus*—are among the species well adapted to urban habitats, supporting our hypothesis that primarily urban-associated species use these farms. Bats that have adapted well to urban habitats can exploit the opportunities offered by human-modified environments, including roosting in buildings and foraging around lights (Ancillotto *et al.*, 2015; Dietz and Kiefer,

2016; Russo and Jones, 2003); therefore, they can readily take advantage of the opportunities provided by livestock farms.

At the same time we also detected the presence of the non-synurbic *B. barbastellus* on livestock farms; this species is typically associated with old-growth forests in good ecological condition and is consequently among the rarer species in Hungary (Dietz and Kiefer, 2016; Görföl *et al.*, 2019; Ruczyński *et al.*, 2010; Russo *et al.*, 2004). Although its activity was low compared with others, its presence in this habitat suggests that a wide range of bat species may benefit from the food resources provided by livestock farms.

Results of Zhan *et al.* (2022) also suggest that cattle farms can represent important foraging areas for many bat species. Around the barns they studied, *P. pipistrellus* occurred most frequently, followed by *Myotis* species, as well as *P. pygmaeus*, *P. nathusii*, *Plecotus* species and *Rhinolophus ferrumequinum*. Based on the experiences from the two studies, several synurbic and dietary generalist species regularly use habitats associated with livestock farming. Differences in species composition between the two studies may reflect regional differences in bat communities, differences in sampling methods, and structural characteristics of the farms.

Bat activity at livestock farms relative to other habitats

Overall bat activity was higher at livestock farms than on arable fields, grasslands, and pine and oak forests, but not higher than on settlement roads or in urban green areas. We also found species-specific patterns: occurrence of *B. barbastellus* and *Myotis* spp. was relatively lower at livestock farms than in forest habitats, whereas activity of *Nyctalus* spp.—which primarily forages in open areas—was higher at livestock farms than in forests and grasslands, indicating that livestock farms provide good foraging opportunities for this taxon. Activity of *P. kuhlii/nathusii* was significantly higher at livestock farms compared with most other habitats; but it did not differ significantly from activity over grasslands and settlement roads. In contrast, *P. pygmaeus* exhibited similar activity levels

across most habitats compared to livestock farms, with lower activity observed only in arable fields.

These results suggest that resource availability and habitat quality at livestock farms are broadly similar to those observed in urbanized habitats. However, it is important to note that the taxa most frequently detected in our study are also common in urban environments. This pattern may be partly explained by the greater availability of potential roost sites in built-up areas, as well as by the proximity of many livestock farms to settlements. In addition, part of the observed differences may reflect methodological effects, as detection probability is generally higher in open habitats such as livestock farms than in closed forests due to more efficient sound propagation. Habitat structure can therefore influence both species occurrence and detectability across habitats (Dietz and Kiefer, 2016; Freeze *et al.*, 2021).

Effects of livestock farm characteristics and landscape composition

Our results—showing that *P. kuhlii/nathusii* were more active at cattle farms than at horse farms—are consistent with Zahn *et al.* (2010), who found that bats preferred foraging in cattle barns compared with horse stables. This may partly be explained by differences in husbandry goals and conditions: cattle are often kept at high densities in more open barns for meat and milk production, whereas horses are kept mainly for recreation and sport in cleaner, more closed stables. Differences in the amount and composition of manure and the associated insect communities may also affect bat activity. Furthermore, the small sample size of horse and mixed farms ($n = 7-8$) limits the generality of the results; therefore, future studies should include a broader range of farm types.

We found a significant relationship between bat activity and the relative proportion of two landscape types—artificial environment, and green areas within the artificial environment—possibly partly because these habitat types were more frequent and thus provided greater statistical power. Within a 250 m buffer around the farm centre, a higher proportion of artificial environment was associated with

higher *Nyctalus* spp. activity, which may be partly explained by the buildings and infrastructure of farms with larger herds. Within the same buffer, the proportion of green areas was positively correlated with total bat activity, suggesting that green area within and around farms are favourable for synurbic taxa such as *P. kuhlii*, *P. pipistrellus* and *Nyctalus noctula* (Ancillotto *et al.*, 2015; Roeleke *et al.*, 2016; Gili *et al.*, 2020; Printz and Jung, 2023). This result may be relevant for the planning and development of livestock farms.

Farms as bat habitats, bats' ecosystem services, and bat-friendly development opportunities

The high bat activity observed on livestock farms suggests that bats' ecosystem services against pests may be valuable on farms as well, in addition to agricultural lands. Outputs of livestock production include, for example, the quantity of milk, meat and eggs, the number of offspring, and overall financial benefit. Insect bites, however, can negatively affect these metrics. The presence of insects and their bites can induce increased stress; bites can cause irritation and acute pain; moreover, insects can transmit viruses, bacteria and endoparasites, leading to diseases that require medical treatment (Baldacchino *et al.*

, 2013; Wichgers Schreur *et al.*, 2021). These health problems not only threaten animal welfare but also increase veterinary costs and farm expenditures, ultimately reducing farmers' income. Most bat species are insectivorous, and in a single night they typically can consume an amount of insects equivalent to 70–84% of their body mass; thus, they can substantially contribute to regulating pest insect populations and mitigate the negative effects of insects on livestock.

At the same time, livestock farms may also pose several risks to bats (Russo *et al.*, 2024). Industrialized farming systems often involve the use of chemicals, drugs and mechanized infrastructure (Mallin *et al.*, 2015; Tullo *et al.*, 2019), which can negatively affect bats directly or indirectly. Pesticides and insecticides may cause lethal or sublethal effects, and their use can also reduce prey availability by suppressing insect populations. In addition, in rural

environments, free-roaming domestic cats represent a significant predation risk for bats. Despite these potential threats, livestock farms can provide suitable or even optimal habitats for bats when designed and managed in a wildlife-friendly manner. By offering favourable foraging conditions and roosting opportunities, such farms can support bat populations, while bats in turn may contribute to the natural regulation of pests (García *et al.*, 2021; Puig-Montserrat *et al.*, 2015).

For more sustainable farming, it is essential to enhance landscape connectivity and habitat diversity, for example by maintaining shrub lines and forest patches and by reducing light and noise pollution. In addition, protecting bats from chemicals and predators, especially domestic cats, is fundamental. It is also important to minimize potential contact between bats and livestock in order to reduce the probability of zoonotic disease transmission (Bonilla-Aldana *et al.*, 2021; Szentiványi *et al.*, 2023). Therefore, it is advisable to create bat roosts farther from livestock facilities—for example in abandoned barns or by placing bat boxes on trees. Through such measures, farmers can help coexistence between bats and livestock, thereby contributing to more sustainable farming practices.

NEW SCIENTIFIC RESULTS

Investigation of the ecological impacts of solar parks on bats

1. To our knowledge, our study is the first to examine the effects of solar parks on bats. We found that bat species typically occurring in urban and agricultural habitats (*H. savii*, *N. noctula* and *P. kuhlii*) are frequently present in solar parks as well, whereas other taxa (*Myotis* spp. and *B. barbastellus*) do not occur, or occur only rarely, in this habitat type.
2. Based on our results, bat communities of solar parks were most similar to those of arable fields, highlighting that bat communities in solar parks most closely resemble the ‘worst’ habitats present in the landscape.

Mitigation options for the deceptive effect of smooth surfaces

1. In our research, we found that the number of bat’s drinking attempts on artificial smooth surfaces can be successfully reduced by placing long, straight, cylindrical objects (e.g., thin strings) on the smooth surface. We supported our findings with behavioural and playback experiments as well as with mathematical modelling.
2. We demonstrated that echo strength—and thus the frequency of bats’ drinking attempts—depends on string diameter and on how the strings are arranged on the surface.
3. Based on the results of mathematical modelling, the frequency of the sound arriving at the surface influences echo strength.

Effects of livestock farm characteristics and landscape composition on bat activity

1. Based on our results, bat activity was significantly influenced by farm characteristics and surrounding landscape composition: *P. kuhlii/nathusii* activity was higher at cattle farms, whereas

Nyctalus spp. activity increased with the proportion of artificial surfaces.

- I. Overall bat activity was positively related to the proportion of green areas within the artificial environment.
- II. Activity of several bat taxa was higher at livestock farms than in agricultural areas and forest habitats; however, forest-associated taxa (*B. barbastellus*, *Myotis* spp.) showed lower activity at farms.

PUBLICATIONS

Publications directly related to the dissertation:

Abdul Rahman NA., Firtha G, **Szabadi KL**, Jones G, Zsebők S (2024). Mitigating the deceptive effects of smooth surfaces: Subtle surface modifications can eliminate maladaptive drinking attempts by bats. *Animal Conservation*, 27(6), 788–801.

<https://doi.org/10.1111/acv.12960>

Szabadi KL, Kurali A, Estók P, Görföl T, Froidevaux JSP, Zsebők S (2025). Bats in livestock farms—Effects of farm characteristics and landscape composition on bat activity.

Landscape Ecology, 40(9), 179. <https://doi.org/10.1007/s10980-025-02196-9>

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Publications related to the subject of the dissertation:

Tinsley E, Froidevaux JSP, Zsebők S, **Szabadi KL**, Jones G (2023). Renewable energies and biodiversity: Impact of ground-mounted solar photovoltaic sites on bat activity.

Journal of Applied Ecology, 60(9), 1752–1762. <https://doi.org/10.1111/1365-2664.14474>

One-page summary in a foreign or Hungarian language – based on a presentation or poster – published in a scientific journal or its supplement.:

Szabadi KL; Kurali A, Estók P, Görföl T, Zsebők S: Denevéraktivitás állattartó gazdaságokban: a telepjellemzők, az épített környezet és a zöldfelületek szerepe, 3. Urbanizációs Ökológia Konferencia, Pécs, Magyarország 2025. október 16-17.

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Kurali A, Kugler P, **Szabadi KL**, Győrössy D, Kriska G, Egri Á, Estók P, Boldogh SA, Görföl T, Bán M, Váczi O, Zsebők S Solar panels and bats: behavioural and ecological investigations to better understand the impact of renewable energy developments on wildlife 16th European Bat Research Symposium Tarragona, Catalonia, Spain, 2024.09.02-2024.09.06 p 161

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