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Mitigating the deceptive effects of smooth surfaces: subtle surface modifications can eliminate maladaptive drinking attempts by bats

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Abstract

The amount of artificial smooth surfaces in the environment increases continuously with urbanization on a global scale. There is growing evidence that smooth surfaces such as windows, solar panels and other objects can serve as sensory traps for many animal species. Artificial smooth surfaces can function as acoustic mirrors, disrupting echolocation of bats and consequently causing maladaptive behaviours such as drinking from and colliding with these surfaces. Therefore, investigating opportunities to mitigate the effects of artificial smooth surfaces is important from a conservation viewpoint. Here, we conducted a field experiment with bats, an ensonification experiment in the laboratory, and a computer simulation, in order to study the effect of mechanical surface modification on the acoustic characteristics of smooth surfaces. In the field experiment, we presented a horizontal smooth plate alone or with strings (diameters between 0.25–2.5 mm) and the behaviour of bats around the plate was video recorded. Bats significantly decreased the frequency of drinking events with increasing diameter of the strings. We also found an indication that a crossed pattern of the strings on the plate may be more effective than a parallel arrangement. The results of the ensonification experiment and the mathematical modelling revealed that a subtle modification of the smooth surfaces with long, linear thin objects can effectively modify the acoustic characteristics of smooth surfaces in general and thereby potentially change the behaviour of bats. Further investigations from sensory, behavioural and ecological viewpoints are proposed to better understand the impact of smooth surfaces on bats and the mitigation solutions that are needed. This research underscores the significance of exploring innovative approaches to minimize the negative impacts of urbanization on wildlife, highlighting the potential of practical interventions to promote coexistence between anthropogenic environments and threatened species.

Introduction

Urbanization and industrialization not only change natural landscapes, but also introduce new challenges to wildlife (Grimm *et al*., 2008; Fenoglio *et al*., 2021). Urban environments can influence reproduction, foraging and resource usage of animals (Lowry, Lill, & Wong, 2013; Villaseñor *et al*., 2014; Ritzel & Gallo, 2020). Different kinds of anthropogenic changes acting through sensory disturbance and deception can lead to maladaptive decisions and reduce fitness (Gwynne & Rentz, 1983; Horváth *et al*., 2009; Cryan *et al*., 2014; Elgert *et al*., 2020). Revealing the sensory mechanisms of animals is essential to develop feasible mitigation techniques and contribute to conservation efforts (Madliger, 2012; Blumstein & Berger-Tal, 2015; Dominoni *et al*., 2020). One of the lesser-known sources of anthropogenic effects is caused by human-made smooth surfaces. The growing number of smooth surfaces such as glass windows and solar panels can introduce serious problems for wildlife. A major cause of avian mortality is the impact of collision with glass buildings (Klem, 1990; Loss *et al*., 2014; Santos, De Abreu, & De Vasconcelos, 2017). Smooth surfaces can also reflect polarized light, and hence aquatic insects often mistake smooth surfaces for water bodies due to their similar light polarization patterns, consequently causing maladaptive reproductive behaviours such as egg-laying over solar panels (Malik *et al*., 2008; Horváth *et al*., 2009, 2010).

The echolocation of bats can also be disrupted by smooth surfaces. Smooth surfaces have acoustic mirror properties, meaning that they reflect calls away from the bats (Greif & Siemers, 2010). While this phenomenon is essential for recognizing water bodies, bats may attempt to drink from smooth surfaces, regardless of the material they are made of, as demonstrated in both laboratory settings (Greif & Siemers, 2010) and in nature (Russo, Cistrone, & Jones, 2012). Additionally, tilted and vertical surfaces can be perceived as open flyways and bats collide with them (Greif *et al*., 2017; Ingeme *et al*., 2018). Greif & Siemers (2010) showed that in experimental situations, bats repeatedly try to drink from the same artificial smooth surface, which indicates that in given circumstances bats may invest considerable amounts of time and energy for unsuccessful drinking attempts. Similarly, repeated collisions with vertical smooth surfaces have been observed in laboratory situations (Greif *et al*., 2017), and serious injuries following collisions into smooth surfaces have been observed in the field (Ingeme *et al*., 2018; Holz *et al*., 2020). While we lack data on the consequences of maladaptive drinking behaviour, collisions with smooth surfaces can directly impact bats' health and consequently, their fitness.

Greif and Siemers (2010) demonstrated in their ensonification experiments that the acoustic properties of smooth surfaces, such as water, plastic, wood and metal, are similar. Consequently, any human-made object with a smooth surface has the potential to pose an orientation challenge for bats. Among the 1474 bat species documented (Simmons & Cirranello., 2024), over 1000 are echolocating bats that regularly visit water bodies each night (Boonman *et al*., 2013; Korine *et al*., 2016), and many have adapted to urban environments (Jung & Threlfall, 2016; Santini *et al*., 2019). Importantly, smooth surfaces are not confined to urban environments; they also extend to areas far from cities. For instance, solar farms are often situated in proximity to agricultural and natural settings, potentially impacting not only urbanized bat species but also those in more rural areas (Barré *et al*., 2023; Szabadi *et al*., 2023; Tinsley *et al*., 2023). This issue gains particular significance in conservation efforts for critically endangered species like the Southern bent-winged bats (*Miniopterus orianae bassanii*) which experience collisions and injuries around metal panels near cave entrances (Ingeme *et al*., 2018; Holz *et al*., 2020).

To reduce the maladaptive effects of smooth surfaces on bats, it is essential to explore effective mitigation approaches. Visual modification of the surface or the environment adjacent to the smooth surface are the most studied approaches. The polarization effect of the surfaces can be modified by white grid patterns (Horváth *et al*., 2010) and insects can be lured away by using beacon lights (Mészáros, Kriska, & Egri, 2021). Smooth surfaces can be changed visually by visible patterns that break up areas of glass to reduce collision risk for birds (Klem, 2009; Sheppard, 2011; Klem & Saenger, 2013). As for bats, recently, lethal effects of wind turbines initiated an intensive search for solutions that can potentially be used to mitigate the effects of smooth surfaces as well. Besides modifying the operating hours and cut-in speeds of turbines depending on the wind speed (Baerwald *et al*., 2009; Wellig *et al*., 2018; Adams, Gulka, & Williams, 2021), other solutions involve exploitation of the bats' acoustic and visual sensory systems. Several studies have investigated the feasibility of acoustic deterrents (Arnett *et al*., 2013; Gilmour *et al*., 2020, 2021), finding moderate or considerable effects as reduced bat activity. Also, combined audio and visual deterrents mounted on drones have shown promise (Werber *et al*., 2022), while the effectiveness of radar as a deterrent still needs further research (Nicholls & Racey, 2007; Gilmour *et al*., 2020). All these bat-related deterrent techniques, however, need considerable technical development and energy use to operate, which can reduce the feasibility of their broad application.

In this study, we focused on a passive acoustic mitigation technique which can work independently of environmental light conditions and which exploits echolocation behaviour – the most important sensory channel for the detection of smooth objects by bats (Greif & Siemers, 2010; Russo, Cistrone, & Jones, 2012). Mostly, the reflection of echolocation signals from insects and spheres (Kober & Schnitzler, 1990; Au & Simmons, 2007; Boonman, Fenton, & Yovel, 2019), and the contrast between smooth and rough surfaces (Greif & Siemers, 2010) have been studied previously. The idea of mechanical surface modification is also supported by phenomena observed in nature. For example, the feeding activity of Daubenton's bats is negatively affected by floating vegetation, leading them to avoid water surfaces covered with dense vegetation (Boonman *et al*., 1998; Ciechanowski *et al*., 2007). However, to the best of our knowledge, there are no studies published investigating the behaviour of bats with the purpose of finding the minimal mechanical surface modification that can change the interpretation of smooth surfaces by bats. In our approach, we focused on the use of long, linear, cylinder-shaped objects that can be easily obtained as threads or strings. Greenfeld *et al*. (2018) prevented bats from accessing the water surface using strings and sheets, both leveraging the detectability of the strings and exploiting the manoeuvrability constraints of the bats. While the physical background of the reflection of sound waves from cylinders is well understood (Morse & Ingard, 1986), we have no empirical evidence about the effectiveness of using such objects as a mitigation solution for the problems that smooth surfaces can cause to bats.

Our objectives were to test empirically the effects of mechanical modification of smooth surfaces on the behaviour of bats and to study the acoustic reflection from these modified surfaces by ensonification and mathematical modelling. We focused our study on bats' perception of water and their corresponding drinking behaviour, as these can be investigated with minimal disturbance compared to experimentally studying collision behaviour. We hypothesized that linear, cylinder-shaped objects with sufficient diameter placed on smooth surfaces can be acoustically reflective and be perceived by bats in such a way that they consequently interpret the surface as not suitable to drink from. We manipulated the diameter of the strings placed on the horizontal smooth surface, predicting that bats would increasingly avoid drinking from the surface with larger string diameters. Concurrently, we predicted observing more intense echoes from larger-diameter strings in both the ensonification experiment and in the modelling. Additionally, in the behavioural experiment, we explored the influence of string arrangement on the smooth surface. Given that most echoes are reflected from smooth objects when sound reaches the surface perpendicularly, we hypothesized that a crossed pattern of strings would increase the likelihood of echoes reaching the bat compared to a parallel arrangement. Consequently, we predicted to observe less drinking activity with the cross-pattern compared to the parallel arrangement of strings. The purpose of the ensonification experiment and mathematical modelling were to generalize our findings to a broad range of surface modifications and bat species.

Materials and methods

Field experiment

The experiments were conducted in the botanical garden of Eötvös Loránd University in Budapest, Hungary (47.4838° N, 19.0855° E) at one of the small ponds (5.30 × 6.80 m) with a water depth of 0.70 m (Fig. 1). Data were collected over 33 evenings from late July until early October in 2020. The experiments were carried out every other night (leaving undisturbed evenings for bats between two experiments), started at sunset and lasted about 90 minutes. Experiments were recorded simultaneously by two normal-speed cameras (Sony HDR-SR5, 50 fps) with night-vision mode. An infrared light was used to illuminate the field of interest in the experiment. On 23 out of the 33 experimental evenings, sound recordings were made by an AudioMoth recorder (OpenAcousticDevices) to characterize the bat activity by species. While we did not record the sound on all the 33 evenings, we believe that based on this sample size we were able to describe the most common bat species and their relative occurrence at the experimental site.

On one side of the pond, we utilized a 1 × 2 m area (the field of interest) where we presented different treatments to the bats (Fig. 1). The first was the control treatment, which was the water surface itself without any artificial objects ($N = 6$ nights). The second treatment was a smooth black plastic plate (1 × 2 m) that was positioned immediately above the water surface without a gap supported by a small table under the surface with adjustable height ($N = 5$ nights). We also presented treatments in which we modified the smooth plate by attaching black plastic strings on the plate surface. The strings were attached parallel to the shorter side of the plate 20 cm apart from each other (9 strings altogether). The diameters of the strings were 0.25, 0.50, 1.00, 1.50 and 2.50 mm ($N = 3$, 5, 3, 3, 3 nights, respectively). An additional treatment was also implemented when the strings with 0.50 mm diameter were placed on the plate in a crossing pattern with the same distances between the strings as at the other treatments (9 strings as in the parallel arrangement +4 additional perpendicular strings, $N = 5$ nights). This procedure resulted in eight different treatments which were presented randomly for each night to account for any habituation of bats to the treatment and to the naturally changing environmental light conditions. It is important to note that lights from the city and the moon could provide some light, a common condition in urban environments, but we believe that the randomized treatments and the black plate with the black strings minimized the effect of the vision of bats for the comparison of the behaviour across the treatments. Prior to the commencement of each trial, the surface of the remaining section of the experimental pond was carefully layered with leaves, effectively limiting the bats to solely engage in drinking attempts within the designated field of interest. The leaves were subsequently removed upon completion of the nightly experiment, providing a suitable drinking area for the bats during nights when no experiments were conducted.

Video and acoustic analysis

All the video recordings were analysed using the Behavioural Observation Research Interactive Software (BORIS, Friard & Gamba, 2016). We determined a 'bat pass' when a bat flew not higher than *c*. 1 m above the field of interest, and we considered only these events in the next steps. Furthermore, we defined 'drinking' as an event when the bat glided over the experimental surface in a head-down position with the lower jaw touching the surface. Note that in the 'drinking' behaviour, bats may touch the plate with their abdomen without abruptly changing their flight track. In contrast, we would define a collision when the bat crashes into the plate, resulting in observable sudden changes in flight direction and speed. Based on the recordings from the two cameras, each capturing different viewpoints, sufficient information was available to accurately determine the categorization of the observed behaviours.

We summed the number of events by category for each night and we calculated the relative occurrence of drinking as the number of 'drinking' events divided by the number of all 'bat passes' for each night. The average length of the recordings was 86.15 ± 3.10 (mean ± SD) minutes. To make an even more balanced dataset, we used the first 80 minutes of recording from each night. Within this length of time, the average number of bat pass events occurring per night was 202.75 ± 131.16.

We analysed the direction of the drinking events in treatment with parallel strings based on the degree between the route of the drinking bats and the strings. For that, based on the recordings from the two cameras, we manually decided whether the bats approached the field of interest in a parallel (0–10 degrees), a diagonal (10–80 degrees) or a perpendicular (80–90 degrees) way. In the parallel situation, bats were approaching the field of interest parallel to the shorter side of the field of interest and so parallel to the strings. Our

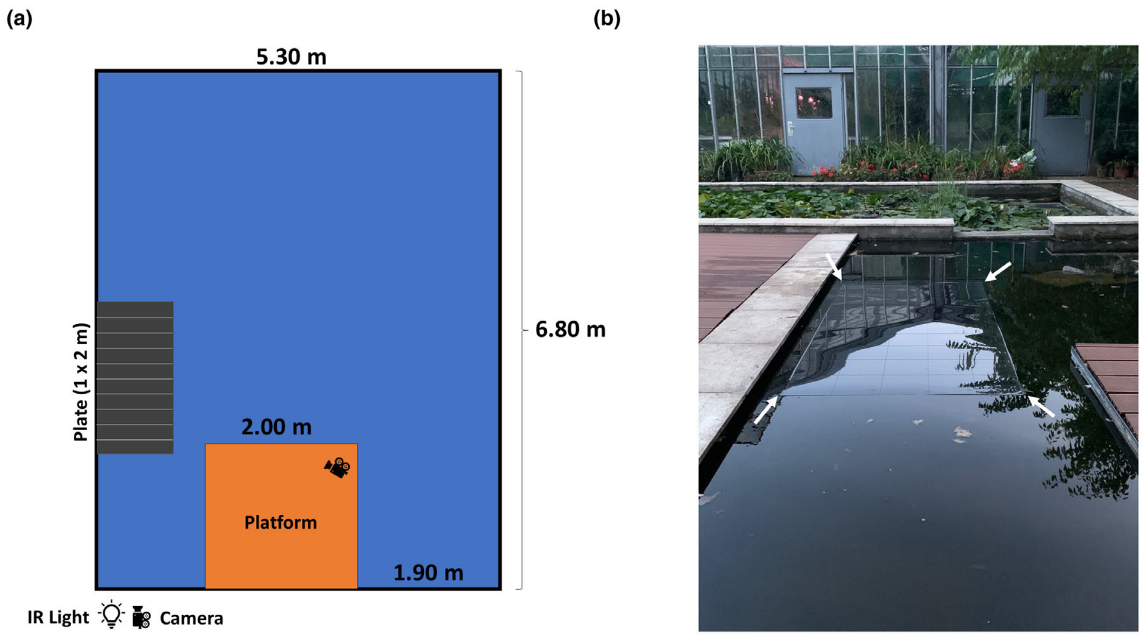

Figure 1 The setup of the behavioural experiment. (a) Arrangement in top view. The dimensions of the pond and the plate are indicated. The place of the plate (field of interest) was illuminated with infrared light. Two night-vision cameras were applied to make video recordings. (b) Photo from the front view with the modified smooth black surface with 0.50 mm strings attached on it in a crossing pattern. The arrows indicate the corners of the plastic plate.

intention was not to accurately measure the degree but to characterize the approximate approach direction and describe the trends across the different treatments.

For the acoustic analysis, we employed the Batdetect program (Mac Aodha *et al*., 2018) to automatically detect bat call sequences. Subsequently, Kaleidoscope Pro (Wildlife Acoustics) software was utilized for the automatic identification of species, with manual verification of the species identification based on Russ (2021). In total, 5312 bat sequences were detected, of which 1867 were successfully identified. The relatively low species identification success rate (35%) was primarily due to the BatDetect program's remarkable effectiveness in detecting bat calls even in very noisy recordings, where species identification was hindered by a low signal-to-noise ratio. Among them, 449 sequences were classified as *Eptesicus serotinus*, and 358 sequences as *Nyctalus noctula*; however, these were excluded from further analyses since they belong to larger species that typically fly at considerable heights. Our focus was on 'bat passes' and 'drinking' behaviour, which were observed exclusively in small-sized bats captured on video recordings. We documented 1002 bat sequences, representing three small-sized bat species (*Hypsugo savii, Pipistrellus kuhlii and P. pipistrellus*).

Unfortunately, we were unable to obtain the data regarding the species-specific outcomes of our behavioural experiment. This is because of the difficulties in identifying species based on the similar echolocation call sequences emitted during the approach phase, compounded by the presence of multiple individuals within the detection range of the audio recorder.

Statistical analysis

We tested the effect of the smooth plate itself by comparing the relative drinking occurrence between the treatments 'water surface' and 'smooth plate without strings'. For that we built a linear model with treatment as a fixed factor and relative occurrence of drinking as the dependent variable by using the 'lm' function in *R 4.1.0* (R Core Team, 2021). The model assumptions in this case, as well as in subsequent cases, were assessed using the *DHARMa* (Hartig, 2021) package.

We tested whether the ratio of drinking at treatments with the thinnest strings (diameter 0.25 mm) was significantly smaller than at the 'smooth plate' treatment. Here, we used a Wilcoxon rank sum test ('wilcox.test' function in R) due to the significantly unbalanced within-group variance.

We also tested our prediction that the diameter of the strings as a continuous variable influenced the drinking behaviour of bats. For that we considered the treatment 'smooth plate' without strings (taking as 0 mm) and all the treatments (0.25, 0.5, 1, 1.5, 2.5 mm) when parallel strings were provided. Considering the decreasing pattern of the ratio of the drinking along the string diameter, we used a non-linear regression approach utilizing the 'drm' function in *drc* package (Ritz *et al*., 2015). We built an exponential decay model according to equation:

$$f(x) = c + (d - c) * exp\left(-\frac{x}{e}\right),$$

where 'c' defines the asymptotic value to which the curve approaches infinity, 'd' determines the initial value of the curve at $x = 0$, and 'e' influences the steepness of the decay. In the model, we included relative occurrence of drinking as a dependent continuous variable and the diameter of the strings as independent continuous variable taking the diameter at the smooth plate treatment without strings as 0 mm.

We also examined the hypothesis regarding the arrangement of the strings. Specifically, we tested whether the drinking ratio was lower in the treatment involving crossed strings compared to parallel strings. As the residual analysis of linear models failed to match assumptions, we applied a Wilcoxon rank sum test with the 'wilcox.test' function, in which we tested the difference between the relative occurrence of drinking in the treatments smooth plate with strings 0.5 mm in parallel and crossed patterns.

All the statistical calculations were done using R. The graphs were made with ggplot2 (Wickham, 2016).

Ensonification

For the ensonification experiment, first, we prepared sound files by using the 'seewave' package (Sueur, Aubin, & Simonis, 2008) in R. Each file contained 100 repeated artificial echolocation calls sweeping down from 150 to 1 kHz with 2 ms duration and 250 ms pause between the calls. This sound file was played back with an ultrasound speaker (Apodemus BatLure, Apodemus Field Equipment, Mheer, Netherlands, ±10 dB SPL 1–100 kHz). The returning echoes were recorded with an ultrasound detector (Pettersson D1000X, Pettersson Elektronik AB, Uppsala, Sweden) at a 500 kHz sampling rate. In this setup, the first string was attached 60 cm far from the shorter edge of the plate, and the further strings were placed 20 cm from each other in parallel (Fig. 2). We ensonified the string sets with the five diameters and the smooth plate in the same arrangement. The speaker and detector were mounted side by side with 9 cm between the centres of the speaker and the microphone. They were fixed on a tripod with the centre of the speaker 23 cm above the plate, 46 cm far from the first string measured in the air and tilted 30 degrees downwards.

In each recorded sound file, we cut the 100 echo series out and aligned to each other by their amplitude curve with a self-made script. For each echo series, we obtained the spectrograms (FFT window length: 256, overlap: 95%) using the 'seewave' package. Next, we calculated the average spectrogram based on the 100 echo series. The resulting spectrograms contained the echoes not only from the strings but also (1) the direct sound from the speaker and (2) the perpendicular echo from the smooth plate. To obtain the spectrograms only with the echoes from the strings, we subtracted the aligned spectrogram of the 'smooth plate without strings' from the spectrograms of the 'plate with the strings'. This procedure resulted in only positive intensity values in the spectrograms where the echoes from the strings were found and hid the other sounds to make clear spectrograms.

Analytical methods

To investigate the individual echo reflections from the strings and the plate separately and to analyse the effect of wire diameter on the echo strength over a wide parameter range, a numerical simulation framework was implemented in the MATLAB 2022b (The MathWorks, Inc.) environment. We analysed two different setups, in which we calculated the reflections (1) from a single string without plate and (2) from a string attached to the smooth surface. The framework allowed the estimation of the reflected wave intensities by solving the acoustic wave equation numerically in the geometry depicted in Fig. S1. The simulation involved the calculation of the harmonic scattered sound fields, reflected from the wire and the plate on an arbitrary source frequency. Since analytical expressions for the reflected fields are available only for infinitely long cylinders and plates, therefore, both the wire and the plate are assumed to be of infinite extent. Furthermore, both the wire and the plate were considered to be acoustically rigid (i.e. the incident wave cannot move them). In the framework, the sound source was modelled as a monopole sound source with undirected sound. The strength of the reflected signal was calculated at the point of the sound source similar to calculations used in the ensonification experiment in which the playback device and the bat detector were close to each other.

The individual echo strengths are calculated based on the acoustic mirror source method Kuttruff (2017) up to reflections of the second order. The first order reflection from the rigid plate below the sound source was calculated by mirroring the sound source to the plate and evaluating the field of the mirror source at the receiver position. For the scattered field of an infinite, rigid cylinder an analytical expression was available, given by equation (4.72) in Williams (1999), allowing the calculation of the first order reflection from the string. Second order reflections (i.e. consequent reflections between the wire and the plate) are modelled by calculating the field of the source scattered from the mirrored wire and the field of the mirror source, scattered from the wire and the mirrored wire. For interested readers the MATLAB code of the simulations can be requested at firtha@hit.bme.hu.

Results

Field experiment

In total, we recorded 6691 bat passes and 688 drinking events from the 33 sample nights based on the video recordings. In the field of interest, we observed 'bat pass' and 'drinking' behaviour only from small-sized bats. Through the acoustic analysis, we identified 1002 echolocation call sequences attributed to small-sized bats across 23 sampled evenings. Among these sequences, 846 (84.4%) were from *Pipistrellus kuhlii*, 119 (11.9%) were from *Hypsugo savii*, and 37 (3.7%) were from *P. pipistrellus*.

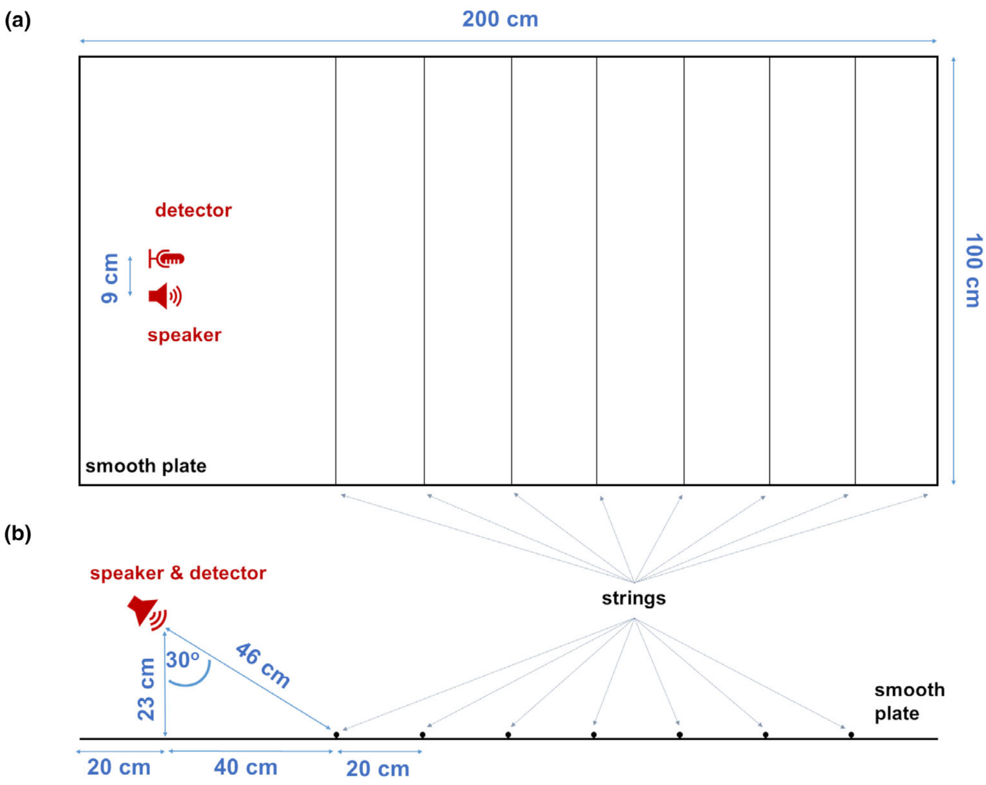

Figure 2 The setup for the ensonification experiment. Both the speaker and the detector were mounted above the ensonified surface and tilted downwards at an angle of 30 degrees in a way that the axis was focused towards the first string. Note that in the ensonification experiment contrarily to the behavioural experiment, we removed the first 2 strings to mimic the water surface in the first part (left side on the picture) of the plate, similarly to a situation when a bat approaching the plate equipped with strings over the water surface.

We did not observe any bats landing or colliding with the plate. Bats showed drinking behaviour at the open water surface in 32% of the bat passes (median) declining to 21% at the smooth plate without strings; however, this difference was statistically not significant (LM, $t = -1.93$, $F_{1,9} = 3.73$, $P = 0.085$, Fig. 3a). The ratio of drinking at 'smooth plate with 0.25 mm strings' was significantly lower than at 'smooth plate without strings' (one-sided Wilcoxon rank sum test, $W = 15$, $P = 0.018$, Fig. 3a).

We found the drinking ratio also significantly lower at the treatment with crossed strings than the treatment with parallel strings (one-sided Wilcoxon rank sum test, $W = 22$, P-value $= 0.022$). There were still some drinking events occurring around the modified plate with a parallel string pattern, but none were observed at the plate with a crossed string pattern plate (Fig. 3b).

When smooth plates with parallel strings are treated, we found a decreasing trend in the ratio of drinking events with increasing diameter of the strings (Fig. 3c). In the treatment with a smooth plate with the thickest strings (2.5 mm) there were no drinking events observed. The parameters 'd' and 'e' of the exponential decay model were found to be significantly different from 0 ($d = 0.208 \pm 0.018$, $t = 11.49$, $P < 0.001$, and $e = 0.167 \pm 0.066$, $t = 2.54$, $P = 0.020$), meaning that compared to the smooth plate stimulus, the treatment with the parallel strings showed a significantly decreasing pattern in the ratio of drinking events with increasing string diameter. Additionally, parameter 'c' was statistically not different from 0 ($c = 0.000 \pm 0.013$, $t = -0.02$, $P = 0.985$), indicating that the exponential decay function approaches 0 and that as the string diameter increases, the drinking rate tends to approach 0. Bats showing drinking behaviour at 0.25 and 0.5 mm approached the plate from all directions, however, we did not observe any perpendicular drinking events at strings with 1–2.5 mm diameter.

The estimation of the approximate flying direction of the drinking bats showed that bats approached the experimental site from all the directions (Fig. S2).

Ensonification

The strength of the echoes was found to be dependent on the diameter of the strings, wherein larger-diameter strings generated stronger echoes (Fig. 4). Consequently, the thinnest strings (0.25 mm) produced considerably weaker echoes in comparison to the thickest strings (2.50 mm). Additionally, a greater number of strings reflected robust echoes, with the reflected echoes containing relatively stronger components in the low frequency range as the string diameter increased. In

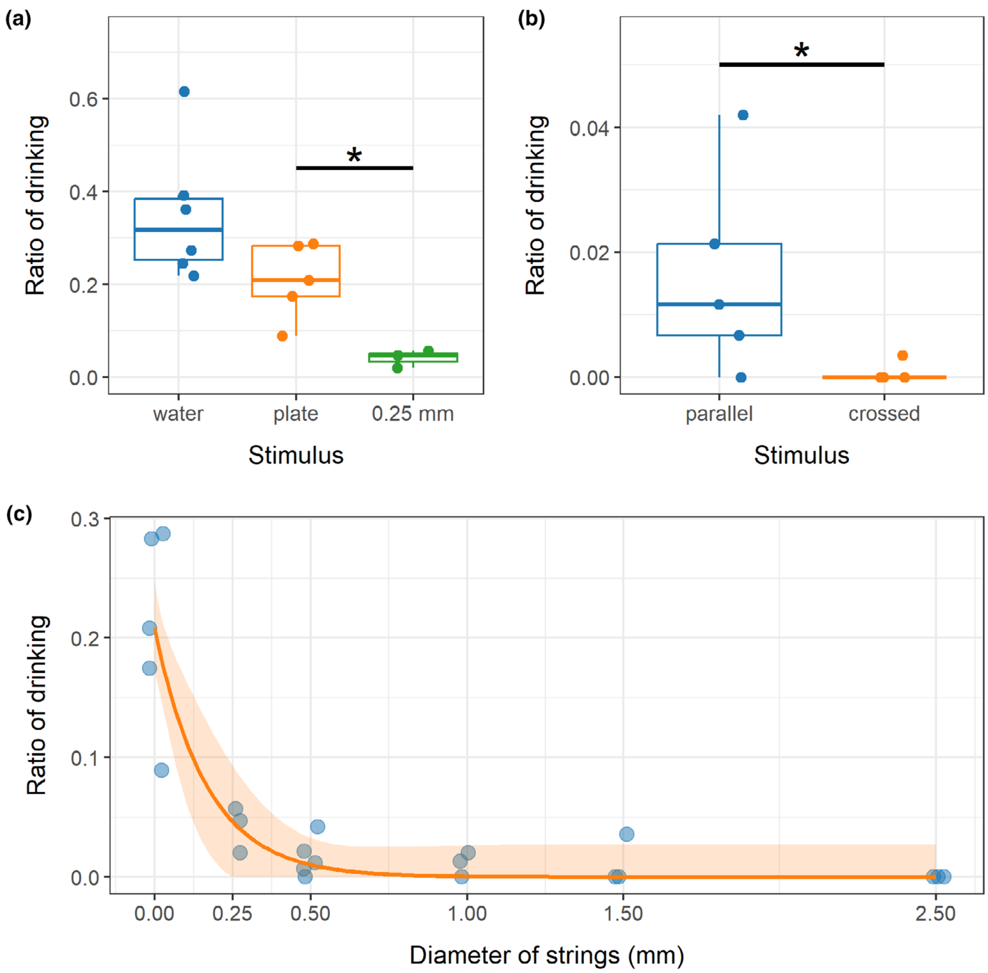

Figure 3 Effects of different treatments on the drinking behaviour of bats. (a) Drinking behaviour of bats over the water, smooth plate without and with strings (diameter 0.25 mm), (b) the effect of the arrangement of the strings attached on the plate (diameter 0.5 mm), (c) exponential decay of the drinking behaviour as a function of string diameter where the smooth plate without strings is shown at 0 mm. Each point represents the drinking ratio calculated for a sampling night based on the number of drinking events and the number of all bat passes. We added some random jitter horizontally to make the data points distinct.

regard to the smooth plate, only the direct signal from the speaker and the signal reflected perpendicularly back from the plate were observed (Fig. S3).

Analytical results

The results of the mathematical calculations revealed clear tendencies about the strength of the reflections as the functions of frequency of the ensonification signal and string diameter (Fig. 5). In accordance with expectations, the strength of the reflected signal increases both with increasing wire diameter and frequency. This tendency is especially clear in the lower frequency range up to 30 kHz at all string diameters and above 30 kHz up to 0.5 mm strings. However, above 30 kHz at strings with diameter 1–5 mm, the strength of the reflected signal already showed some decreasing trends. At strings with 1 mm, the intensity started to decrease above 90 kHz, while strings with diameter 2.50 and 5 mm reflected the echo with large variance.

The strength of the perpendicular echo from the smooth plane showed only a slight decrease as frequency increased along the studied frequency range and was around 15 dB higher than the strongest echo of the strings. The strength of the reflected signals was around 10 dB higher in cases where the strings were placed on the smooth surface compared with when they were presented alone without a smooth surface (Fig. 5a vs. Fig. 5b).

Discussion

In summary, we found that drinking behaviour of bats from artificial smooth surfaces can be mitigated by arranging long, linear, cylinder-shaped objects with small diameters (e.g. thin strings) on the smooth surface. Increase in the string

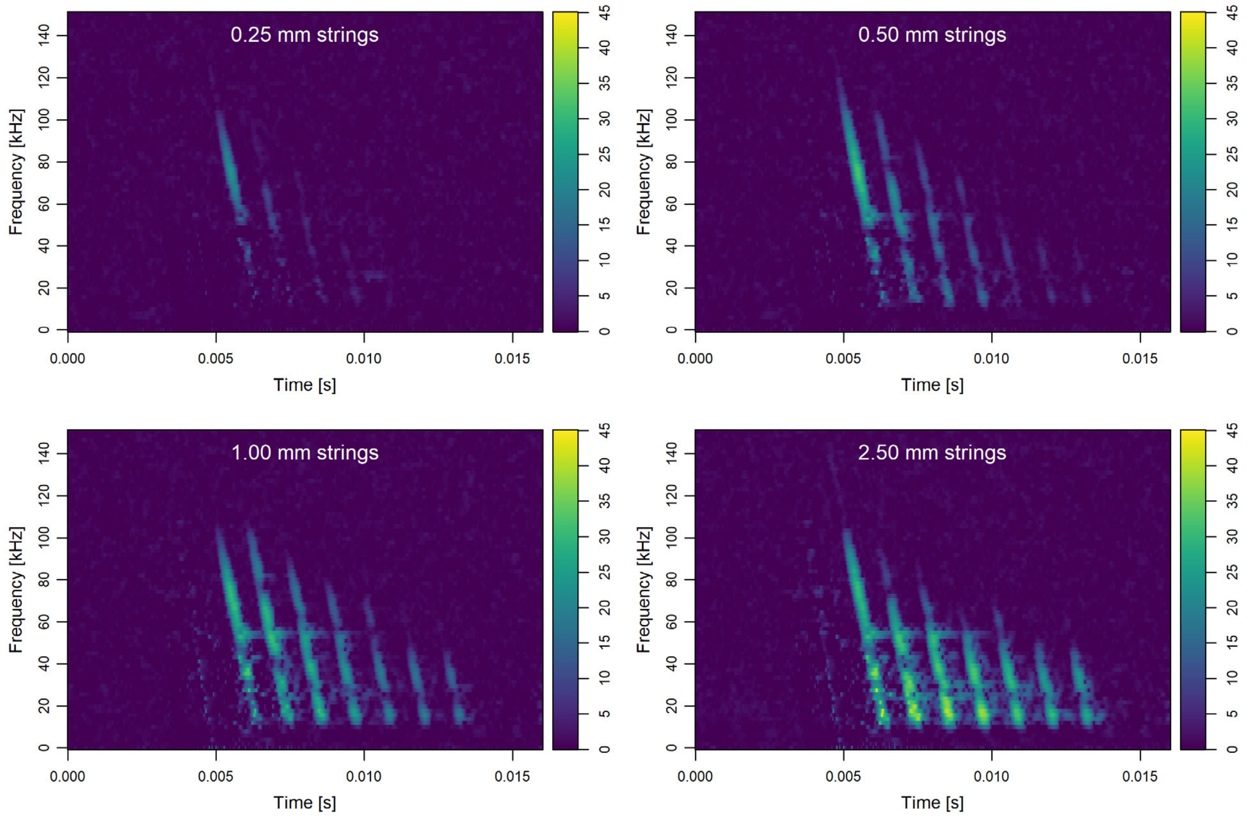

Figure 4 Echo spectrograms of the ensonification experiment. Only the echoes from the strings are shown. The colour bars show the relative amplitude of the signals in dB after subtracting the spectrograms of strings from the spectrogram of the smooth plate.

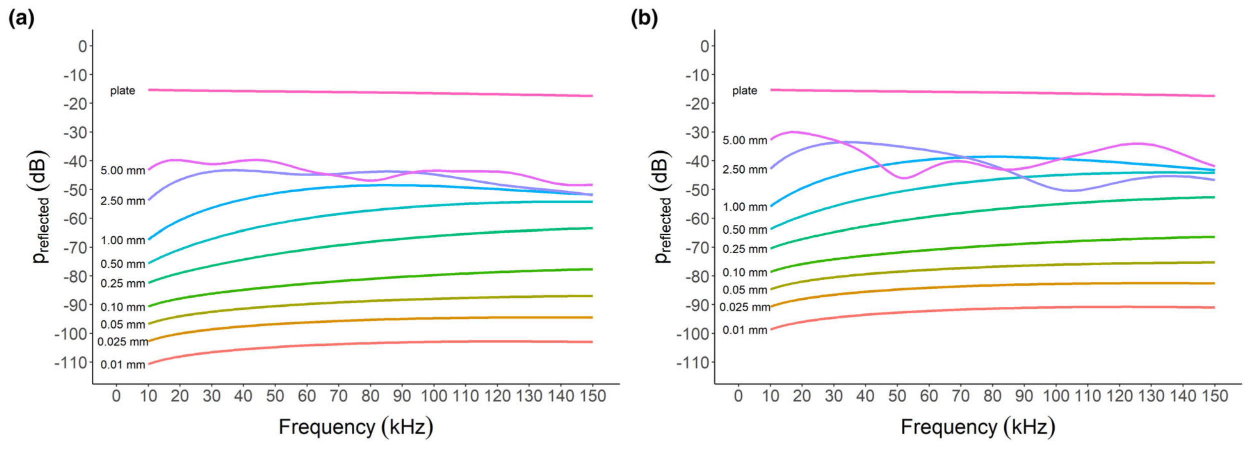

Figure 5 Analytical results of the acoustic reflections from the strings with different diameters. The calculations were performed for (a) strings without plate and (b) strings placed on the surface of smooth plate modelling a non-directed ensonification situation. Reflections from the smooth plane are also represented for reference. The colours of the lines indicate the strings with the different diameters (0.01–5 mm) and the smooth plate.

diameter intensified the mitigation effect, and this finding was also supported by the ensonification experiment and mathematical modelling. We also found empirical evidence that employing a crossed-patterned configuration of strings, maintaining the same distances between them as in the parallel arrangement, can further contribute to the mitigation effect.

We observed a considerable increase in the echo strength as the diameter of the strings increased in both the ensonification experiment and the mathematical modelling.

Accordingly, in the behavioural experiment, the drinking ratio showed a non-linear decreasing trend with increasing string diameter. At the experimental site, three small-sized bat species appeared (*H. savii, P. kuhlii and P. pipistrellus*) typically emitting echolocation calls with maximum energy between 32 and 50 kHz (Russo & Jones, 2002). This is similar to the findings of Sümer, Denzinger, & Schnitzler (2009), who studied big brown bats (*Eptesicus fuscus*) emitting calls with the highest amplitude between 35 and 45 kHz. The behavioural responses of this species also demonstrated non-linearity based on vertically arranged strings, exhibiting the greatest change below a string diameter of 0.5 mm, similar to our results. Also in agreement with our results, Greenfeld *et al*. (2018) found that horizontally placed strings with a diameter of 2 mm were easily detectable for *P. kuhlii*. Beyond that, our results suggest that bats are able to perceive the difference between smooth surfaces with and without strings of 0.25 mm in diameter, as the drinking rate significantly decreased in the case of strings placed on the smooth plate. Previous studies investigating the detection of vertical strings in the air found that for *Asellia tridens* wires with diameter of 0.05 mm (Gustafson & Schnitzler, 1979) and 0.2 mm for *Eptesicus fuscus* were already detectable (Sümer, Denzinger, & Schnitzler, 2009).

Both the results of the ensonification experiment and the mathematical calculations showed that the echo strength depended on the frequency of the sound. In general, we found approximately 5–10 dB increases in echo strength from 10 to 150 kHz explicable by the shorter wavelength of the signal at higher frequencies causing larger reflectance (Morse & Ingard, 1986; Pye, 1993; Houston, Boonman, & Jones, 2004). However, above 0.5 mm string diameter, interference phenomena resulted in strong fluctuation in the echo intensity, manifesting in an apparent intensity decrease (Morse & Ingard, 1986; Pye, 1993). Also, with the smooth plate without strings, the slight decrease in echo strength with increasing frequency was probably due to increased atmospheric attenuation at high frequencies. Consequently, these results suggest that further increases of string diameter especially above 1 mm mainly contribute to echo strength in the low frequency range. For mitigation targeting specific bat species, this phenomenon should be considered, ensuring that the string diameter aligns well with the wavelengths of the calls emitted in by the species of concern. In our ensonification experiment, not only did the intensity of the echo from the first string increase, but the subsequent strings in the string set also became more detectable with increasing string diameter. Therefore, these results suggest that a string set with a sufficient diameter reflects an echo series as an inhomogeneous surface.

We lack the data on species-specific results from our behavioural experiment due to technological constraints. However, based on the results of analytical modelling, we expect only a small difference (approximately 5 dB or less) in the reflectance of a string with a given diameter within the frequency range of maximum energy (32–50 kHz) for the three species potentially present in our experiment. Consequently, we do not predict significant differences in the drinking behaviour of these species. Additionally, we suggest that drinking behaviour of other bat species with call frequencies within this range or higher could be reduced already with a minimum string diameter of 0.25 mm on surfaces.

The mathematical calculations showed that strings placed on a smooth surface have around 10 dB stronger reflections compared to strings without the surface. The explanation of this is that not only the echo of the string itself but also the reflection of the string from the surface increases the target strength. This has been previously described in the ensonification experiment by Siemers, Stilz, & Schnitzler (2001) related to mealworms, a phenomenon that increases the detection of prey items on smooth surfaces by trawling bats (Siemers, Baur, & Schnitzler, 2005). Accordingly, as this acoustic mirror effect can contribute to the detection of strings placed on smooth surfaces, it is advisable to exploit this phenomenon in the design of attaching strings on such surfaces or in other mitigation approaches in future.

We also found that the arrangement of the strings can influence the mitigation effect. Based on the video recordings we observed that bats approached the drinking site from different directions. In theory, we expect the greatest reflection from the strings towards the sound source when the sound reaches the strings perpendicularly. Therefore, we expected higher probability of pronounced echoes from the string set in cases where the strings are arranged in a crossed pattern. Accordingly, we observed a statistically lower number of drinking events of bats arriving from different directions when the strings were arranged in the crossed compared to the parallel pattern. Consequently, future mitigation efforts should consider utilizing a string set with reflective strings arranged in multiple directions.

While this study primarily focused on mitigating the drinking behaviour of bats at horizontal smooth surfaces, it is crucial to extrapolate our findings to angled smooth surfaces. Currently, there is a lack of published studies examining the behaviour of bats at smooth surfaces inclined between 0 and 45 degrees, despite documented collisions with smooth surfaces at 45 and 90 degrees (Greif *et al*., 2017; Ingeme *et al*., 2018). Drawing on the acoustic mirror phenomenon, Greif *et al*. (2017) propose that bats interpret smooth surfaces as water when receiving a weak echo from below and no echo from the front. This phenomenon remains applicable even when the smooth surface is at an acute angle to the horizontal. Consequently, we anticipate observing drinking behaviour in bats on smooth surfaces at angles below 45 degrees—a hypothesis that warrants experimental exploration. In this study, we demonstrated that thin strings on a smooth surface can effectively reflect bat sounds. The extent of this reflection depends mainly on the angle between the sound source and the orientation of the strings, and we predict similar reflection outcomes, irrespective of the angle of the smooth surface relative to the horizontal. Consequently, if bats approach a smooth surface oriented at any angle in which reflective strings are mounted, we predict that the acoustic cues will be helpful to the bats in their orientation. Therefore, we anticipate that both drinking behaviour and collision events can be mitigated in such circumstances.

From a practical standpoint, it is crucial to determine which surfaces can be considered smooth and hence merit attention. In our study, we successfully replicated the smoothness of water surface using a smooth plastic plate, as demonstrated by the absence of a significant difference in drinking behaviour observed in bats between these two surfaces. Greif & Siemers (2010) revealed that the acoustic mirror phenomenon is independent of the material a smooth object is made of, suggesting that any human-made smooth object has the potential to cause orientation problems for bats. While Smotherman, Croft, & Macias (2022) conducted ensonification and behavioural experiments with surfaces of quantified roughness, their focus did not extend to investigating the acoustic mirror properties of the surfaces. It is imperative to conduct similar studies that quantitatively determine the roughness of smooth surfaces in the anthropogenic environment and comprehend their acoustic properties. Furthermore, it is essential to acknowledge that the smoothness of the surfaces of ordinary objects can vary by manufacturer. For example, in solar panels, the glass surfaces may be coated in diverse ways (Mozumder *et al*., 2019). Despite the intended smoothness of these surfaces, they may exhibit slight variations in roughness, leading to differing acoustic properties. This highlights the necessity of further research in this direction.

We propose a three-step mitigation plan in which, firstly, potentially problematic smooth surfaces should be identified; secondly, mitigating objects should be applied to these surfaces; and finally, close monitoring of the surfaces should be conducted by recording changes in bat behaviour. Potentially, all extensive smooth surfaces at various angles, such as windows, solar panels or glass, plastic, or metal surfaces frequently found in anthropogenic environments, may disrupt bat navigation. Consequently, it is impossible to modify the surfaces of all such objects. The strong innate water recognition, primarily based on acoustic cues in bats, leads individuals to attempt drinking from horizontal smooth artificial surfaces, often repeatedly (Greif & Siemers, 2010). However, Russo, Cistrone, & Jones (2012) recorded only some repeated attempts from each individual at drinking from artificial smooth surfaces placed over drinking sites in nature. This indicates that bats try to change their drinking locations in case of unsuccessful attempts. Accordingly, we believe that maladaptive drinking behaviour can be primarily energy-demanding, especially in cases where the ratio of artificial smooth surfaces is considerably higher than that of natural water surfaces. This phenomenon is more likely to occur in anthropogenic and arid environments, suggesting a potentially energy-demanding situation for bats, for example, in the case of solar farms in deserts.

To identify the potentially problematic localization of smooth surfaces, one of the most relevant factors might be their vicinity from bat colonies and hibernation sites. Ingeme *et al*. (2018) observed frequent collisions of bats with a metal plate, especially in juvenile individuals, suggesting the role of experience in avoiding collisions with smooth surfaces. Similarly, we anticipate that smooth surfaces on the commuting routes of bats might increase the likelihood of encounters. Additionally, as detailed above, artificial smooth surfaces with angles close to horizontal, especially in arid environments, might pose challenges for bats in locating water surfaces; therefore, it might be advantageous to apply mitigation techniques. As for surface modification, conservation efforts should consider the target bat species and the frequency of its echolocation calls in the choice of the string diameters. However, if the application of a string set with large string diameter is feasible, then it is advisable to choose strings with large diameters that are predicted to mitigate the effect of the smooth plate for all echolocating bat species independently of their call characteristics. While we used 20 cm spacing in our experiment, and it was found to be appropriate for *Pipistrellus/Hypsugo* species, we also predict that smaller spacing can even increase the mitigation effect, as this increases the reflective surface. We suggest that our approach can be used broadly on smooth surfaces in situations when the surface cannot be modified in other ways by placing a thin visible and rough acoustical thread on the targeted surface. However, we encourage manufacturers of products with smooth surfaces to produce bat-friendly surfaces by considering the results of our and future studies focusing on the acoustic characteristics of the surfaces and the sensory ecology of bats.

Further research should also focus on the visual cues that may contribute to the orientation of bats alongside acoustic cues, as the integration of audio and visual cues may further enhance the mitigation of the effects of smooth surfaces. While Russo, Cistrone, & Jones (2012) did not find an observable effect of the colour of the smooth artificial surface, it has been shown that a linear-shaped light beam affects obstacle avoidance by *Eptesicus fuscus* (Jones & Moss, 2021) and that foraging for moths is affected by moth colour (white vs. dark) in *E. nilssoni* (Jensen, Miller, & Rydell, 2001; Eklöf, Svensson, & Rydell, 2002), suggesting that further investigations into the impact of visual patterns could be advantageous for mitigation. While we lack knowledge about the role of ambient light in water recognition, previous studies have shown that bats integrate visual and echo-acoustic information in their orientation (Orbach & Fenton, 2010; Salles, 2022). This latter phenomenon may assist bats in recognizing artificial smooth surfaces in general when exposed to natural or artificial ambient light.

Our results indicate that distantly spaced thin linear objects can be effective in mitigation. Such linear structures may occupy a relatively small portion of the surface, which could allow for the development of applications that minimally impact visibility through glass or the energy transmission of solar panels. It is important to note that the application of linear structures in light colours can have additional effects by mitigating the impact of polarized light pollution. This, in turn, decreases the attraction of insects, especially when applied on black smooth surfaces like solar panels (Horváth et al., 2010). Additionally, as visual patterns can successfully mitigate collisions of birds with windows (Rössler, Nemeth, & Bruckner, 2015; Sheppard, 2019; Ribeiro & Piratelli, 2020), it may be advantageous to develop such surface patterns that serve as cues for multiple animal taxa. As strings or other thin linear objects can be mounted easily on many smooth surfaces, this approach can be applied even after the installation of the smooth surfaces, similarly to the patterns used for mitigating bird collisions with windows.

In conclusion, we have demonstrated an effective mitigation solution for the effects of smooth surfaces in this study, supported by behavioural and ensonification experiments, as well as analytical modelling. While the application of thin cylinder-shaped objects mounted on smooth surfaces appears feasible, numerous questions remain open and necessitate extensive research at the sensory and behavioural levels. Furthermore, additional investigation is needed at the ecological level to assess the fitness consequences of smooth surfaces. Recent studies examining movement and foraging behaviours of bats in environments with extensive artificial surfaces, such as solar farms, have already demonstrated species-specific ecological effects and underscored the significance of further ecological research (Barré *et al*., 2023; Szabadi *et al*., 2023; Tinsley *et al*., 2023).

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Authors' contributions

G.F., N.A.A.R. and S.Z. conceived the ideas and designed the methodology; N.A.A.R. and S.Z. conducted the experiments; G.F. conducted the computer simulations; N.A.A.R. and S.Z. analysed the data; all authors contributed to the writing, reviewing, editing and finalizing of the manuscript.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Geometry for numerical acoustical simulations. For the detailed description, see Methods.

Figure S2. Direction of drinking events. We summed all the drinking events up in the treatments with different parallel strings. The colours indicate the approximate approaching direction to the shorter side of the plate (same as the direction of the parallel strings).

Figure S3. Spectrograms of the ensonification experiment. The spectrograms contain the echoes from the speaker (1st signal) and perpendicular echoes from the surface below (2nd signal), and all the echoes from the strings (starting from the 3^{rd} signal).