Effects of Wind Turbine Noise on Songbird Behavior During Nonbreeding Season

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Conservation Biology

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Abstract

Anthropogenic noise is one of the fastest growing, globally widespread pollutants, affecting countless species worldwide. Despite accumulating evidence of the negative impacts of wind turbines on wildlife, little is known about how the noise they generate affects ecological systems. Songbirds may be susceptible to noise pollution due to their reliance on vocal communication and thus, in this field study, we examined how songbirds are affected by wind turbine noise. We broadcasted noise produced by one wind turbine in a migratory stopover site during the nonbreeding season. Throughout the study, we repeatedly monitored the acoustic environment and songbird community before, during, and after the noise treatments with passive acoustic monitoring and mist netting. We employed generalized linear mixed effects models to assess the impact of experimental noise treatment on birds behavior and likelihood ratio tests to compare models with variables of interest with null models. The daily number of birds in the presence of wind turbine noise decreased by approximately 30% compared with the before and after phases. This reduction had a significant spatial pattern; the largest decrease was closer to the speaker and on its downwind side, fitting measured sound propagation. Although we found no impact on species diversity, two out of three most common species showed clear avoidance behavior: 45% and 36% decrease in abundance for the lesser whitethroat (*Sylvia curruca*) and Sardinian warbler (*Sylvia melanocephala momus*), respectively. In the after phase, there were lingering effects on the lesser whitethroat. The age structure of the lesser whitethroat population was affected because only juvenile birds showed avoidance behavior. No difference in avoidance extent was found between migratory and nonmigratory species, but the impacts of displacement on migrants during stopover are especially troubling from a conservation perspective. Our results stress the need to address the impacts of noise pollution on wildlife when planning noise-generating infrastructures, such as wind turbines, to allow for sustainable development without threatening already declining songbird populations.

KEYWORDS

anthropogenic noise, avoidance behavior, bird migration, conservation behavior, renewable energy, stopover ecology, warblers, wind turbines

Resumen

El ruido antropogénico es uno de los contaminantes con mayor crecimiento y distribución a nivel mundial, por lo que afecta a incontables especies en todo el mundo. A pesar de acumular evidencia sobre el impacto negativo que tienen las turbinas eólicas sobre la fauna, se sabe muy poco sobre cómo el ruido que generan afecta a los sistemas ecológicos. Las aves canoras pueden ser susceptibles a la contaminación sonora ya que dependen de la

comunicación vocal y, por lo tanto, en este estudio de campo, analizamos cómo les afecta el sonido producido por las turbinas eólicas. Transmitimos ruido producido por una turbina en un punto de parada migratorio durante la temporada no reproductiva. Durante el estudio, monitoreamos repetidas veces el entorno acústico y la comunidad de aves canoras antes, durante y después de los tratamientos de ruido con monitoreo acústico pasivo y redes de niebla. Empleamos modelos de efectos lineales mixtos generalizados para evaluar el impacto del ruido experimental sobre el comportamiento de las aves y pruebas de probabilidad de proporción para comparar los modelos con variables de interés con los modelos nulos. El número diario de aves en la presencia del ruido de turbinas eólicas disminuyó aproximadamente un 30% en comparación con las fases de antes y después. Esta reducción tuvo un patrón espacial significativo: la mayor disminución ocurrió más cerca a la bocina y en el lado de sotavento, lo que se ajusta a la medida de la propagación del sonido. Aunque no encontramos impacto alguno sobre la diversidad de especies, dos de tres de las especies más comunes mostraron un comportamiento de evasión evidente: 45% y 36% de disminución en la abundancia de *Sylvia curruca* y *Sylvia melanocephala momus*, respectivamente. Durante la fase posterior al ruido, observamos efectos prolongados en *S. curruca*. La composición de edades de la población de *S. curruca* se vio afectada porque sólo los individuos juveniles mostraron un comportamiento de evasión. No encontramos una diferencia en el grado de evasión entre las especies migratorias y no migratorias, pero el impacto del traslado sobre las migrantes durante el punto de parada es de preocupación especial desde una perspectiva de conservación. Nuestros resultados acentúan la necesidad de abordar el impacto de la contaminación sonora sobre la fauna cuando se planean estructuras que producen ruido, como las turbinas eólicas, para permitir el desarrollo sustentable sin amenazar a las poblaciones de aves canoras que ya están en declive.

Efectos del ruido de turbinas eólicas sobre el comportamiento de las aves canoras durante la temporada no reproductiva

INTRODUCTION

In recent decades, evidence of various negative impacts of wind turbines on birds has accumulated (e.g., increased mortality, reduced breeding success, altered feeding rate, and lower population densities) (Allison et al., 2019; Dai et al., 2015; May et al., 2017; Shaffer & Buhl, 2016), yet the mechanisms behind these impacts remain unclear. Better understanding of the factors contributing to these negative impacts is key for the development of applicable mitigation tools (May et al., 2017) and for better planning and placement of infrastructure. Without empirical evidence, some researchers have suggested that wind turbine noise may play a major role in displacing birds from their habitats (Dooling, 2002; Stevens et al., 2013; Wang et al., 2015; Zwart et al., 2016).

Animals use acoustic information from their surroundings to assess habitat quality and resource distribution (Farina et al., 2011; Pijanowski et al., 2011). Recent decades have brought a rapid increase in anthropogenic sounds (Barber et al., 2010), commonly termed *noise pollution*. This pervasive and important human-caused element degrades habitat quality and affects many species worldwide, even in supposed refuges, such as protected areas (Buxton et al., 2017; Senzaki et al., 2020a; Swaddle et al., 2015). Noise can be perceived as a threat by animals, it

may distract them and reduce the efficiency of their actions, and it may mask their communication, obscuring acoustic signals upon which they may rely (Dominoni et al., 2020). A common behavioral reaction to noise pollution is avoidance of noise-polluted areas (Cinto Mejia et al., 2019; McClure et al., 2013; Shannon et al., 2016). Displacement caused by noise reduces the availability of habitat, potentially forcing individuals into habitats of lower quality. Even if an individual stays in a disturbed habitat, it does not mean it is not subject to the negative effects of this disturbance (Dominoni et al., 2020; Swaddle et al., 2015).

To successfully use their environment, animals must optimize their rate of information gain to maximize their exploitation of resources in ever-changing habitats (Berger-Tal et al., 2014). This is especially true for migrating and dispersing individuals for which the environment may be completely novel. Specifically, many birds rely on vocal cues for stopover site selection (Mukhin et al., 2008; Németh & Moore, 2014) and for decision-making within sites (Németh & Moore, 2007). However, exposure to noise pollution might disrupt these crucial communication behaviors (Barber et al., 2010; Shannon et al., 2016), leading to a reduction in perceived habitat quality and increasing the chances that individuals will avoid the area (Cinto Mejia et al., 2019; McClure et al., 2013; Shannon et al., 2016). Such behavioral changes can scale up from the individual level

by modifying population structure, shaping communities and, in the long run, altering entire ecosystems (Francis & Barber, 2013).

A rapidly growing source of noise pollution worldwide is wind turbines (Dai et al., 2015; Zwart et al., 2016). Despite their recognized environmental benefits, wind turbines can negatively affect wildlife populations through direct mortality and disturbance or by reducing breeding success, altering movement patterns, and causing large-scale habitat loss via avoidance (Dai et al., 2015; Fernández-Bellon et al., 2019; May, 2015; Stevens et al., 2013; Wang et al., 2015; Zwart et al., 2015). Specifically, wind turbine noise substantially increases ambient sound levels (Dai et al., 2015) within the hearing range of many animals, including most bird species (Dooling, 2002). The magnitude of noise created by a wind turbine can remain above 30 dBA (A-weighted decibels) even at a distance of 800 m (Katinas et al., 2016; Rogers et al., 2006). This distance (800 m) fits the range of avoidance behavior found in several wind turbine studies (Percival, 2005; Fernández-Bellon et al., 2019; Santos et al., 2021). Moreover, wind turbine noise differs from other sources in three important aspects when considering noise impacts on the acoustic environment or on wildlife (Gomes et al., 2021): it is noticeable even when the measured level is below the natural background sound level because of its amplitude modulation (a repeating swooshing sound with regularly repeated peaks higher by 15–20 dB compared with minimum sound pressure level (SPL) at different frequency bands [Katinas et al., 2016]); it has a broadband frequency range (mainly 1–5 kHz but often reaching 8 kHz and more [Dai et al., 2015; Katinas et al., 2016]); and it is influenced by wind conditions (Rogers et al., 2006). These factors lead to an unpredictable variation between hours and days, and they distinguish wind turbine noise from traffic noise, for example (Pedersen & Van Den Berg, 2010), the most extensively studied source of anthropogenic noise (Jerem & Mathews, 2021). Altogether, the high intensity and the unique acoustic signature make it an obvious knowledge gap in the noise-pollution literature and limit understanding of the possible impacts of such noise on the movement and the habitat selection of wildlife (May et al., 2017; Zwart et al., 2015).

Although studies examining bird mortality as a result of collisions with turbines are relatively abundant, only a few have investigated the displacement of birds due to nonlethal impacts of windfarms (Coppes et al., 2020; Taubmann et al., 2021). Studies investigating the effects of turbine-generated noise on birds are even fewer and mostly focus on breeding behavior (Gómez-Catasús et al., 2022; Szymański et al., 2017; Whalen et al., 2019). The limited available literature suggests that wind turbine noise affects bird vocal communication and habitat use (Gómez-Catasús et al., 2022; Szymański et al., 2017; Whalen et al., 2019; Zwart et al., 2016). Attempts to estimate the spatial extent of avoidance of wind turbines by birds, possibly but not necessarily due to noise, show varying results; some species exhibit larger avoidance distances than others (ranging from several dozens to 850 m). Variation in the range of impact among species, including closely related ones, may be attributed to life history of the species, internal state factors (e.g., age and sex biases), windfarm location, or microsite conditions within an individual windfarm (Fernández-Bellon et al., 2019; Percival, 2005; Santos et al., 2021). In the absence of empirical data on the impact of wind turbine noise pollution on migratory songbirds, the conservation of vital stopover sites may be hampered. To fill this knowledge gap, we broadcasted the sound of a wind turbine in a migratory stopover site during the nonbreeding (migration) season to quantify the effects of wind turbine noise on the natural acoustic environment and consequently, on songbird species diversity, population structure, and avoidance behavior.

METHODS

We tested the effects of wind turbine noise on songbirds by creating a phantom wind turbine (sensu McClure et al.'s, 2013 "phantom-road" experiment): an acoustic experimental manipulation based on broadcasting wind turbine noise that isolated the effects of noise from other effects, such as visual or tactile cues. We measured the surrounding acoustic environment and the status of the songbird community before, during, and after the noise treatment.

We repeated the experiment six times; each repeat included three 48-h phases (before, noise treatment, and after). We did not take measurements on Saturdays, which are the national weekend in Israel and may thus be characterized by different human-induced background noise levels. We repeated the experiment every second week to allow migratory birds to continue their migration and for new birds to arrive. Similarly, nonmigratory species were able to redistribute naturally in the habitat between repeats. The 1-week gap between each experimental repeat ensured that we tested a different migratory bird community every time (and this was supported by the extremely low recapture incidents of marked individuals between repeats [Appendices S2 & S3]), thus allowing the use of a single site and eliminating among-site variation (in species composition and in noise propagation due to differences in topography, but see "Study Limitations"). Overall, we conducted six repeats of the experimental protocol during the fall of 2018, from 20 August to 2 November (postbreeding or migration).

Study site

We conducted our study at Horesh Adulam Nature Reserve in central Israel (Figure 1a). This migratory stopover site is characterized by a generally homogenous Mediterranean Maquis habitat enclosed by three minor roads. The closest human settlement is a small village 1.5 km distance. These conditions make this a quiet site (Appendix S4) and thus ideal for sound recordings and manipulations. Weather measurements (including wind direction and speed) were obtained from the nearest weather station, situated <4 km away at Beit Govrin, with a clear line of sight to the study site (Vantage Pro2 Plus, Davis Instruments; Weather station data available on Wunderground.com, station ID IDAROMBE2). We calculated the average hourly wind speed for all monitoring hours.
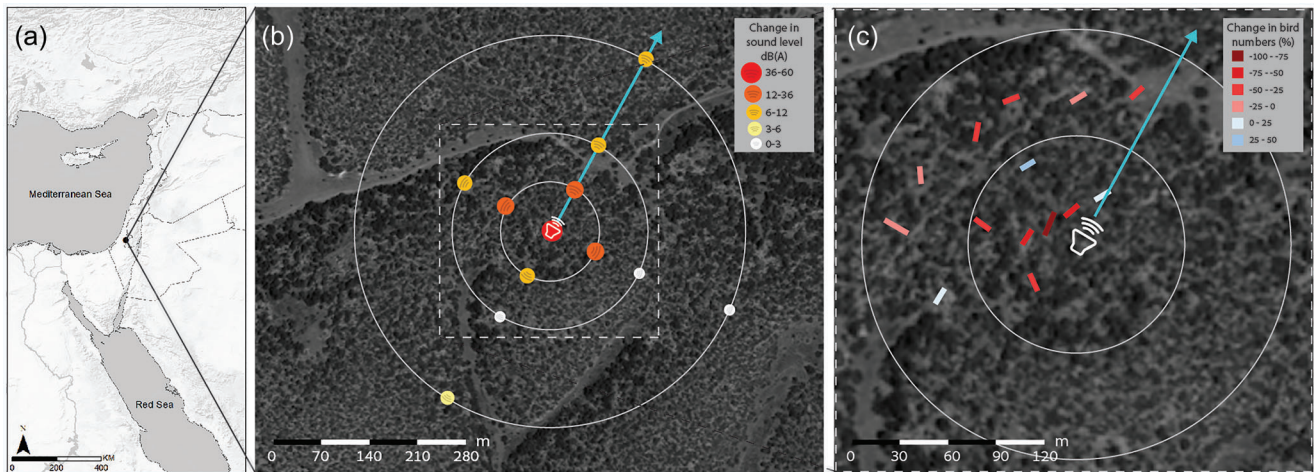
FIGURE 1 (a) Location of Horesh Adulam Nature Reserve study site (black dot) in central Israel, (b) change in ambient sound level between the wind turbine noise treatment and before the treatment calculated as the difference between the mean L_{50} (median) noise level in dBA measured during bird-ringing hours (Appendix S5) (after phase absent due to its similarity to the before phase; colors on the red spectrum, larger changes in sound levels; gray circles, 70, 140, and 280 m from speaker; dashed square, area enlarged in [c]), and (c) change in number of birds between noise treatment and before noise treatment phases, as measured by the reduction of the mean number of birds between these two phases, according to sampling location (mist nets) (after phase absent as in [b]; dark red, stronger decline in the number of birds; blue, increase in the number of birds; blue arrow, sound direction based on expected downwind side; see statistical model in Table 2).

Phantom wind turbine

To create the phantom turbine during noise-treatment days, we broadcasted wind turbine noise (Appendix S1) at a typical level of 102 dBA L_{eq} (Katinas et al., 2016), which we measured for 30 s 1 m from the speaker (Soundboks2, 40–20,000 Hz, Soundboks). The WAV files of wind turbine noise recordings were provided by Timothy Van Renterghem (for recording details, see Van Renterghem et al., 2013) and were played using a SanDisk Clip player. The recording accurately recreates real wind turbine noise with respect to the range of frequencies and amplitudes that are relevant to the avian and the human auditory system. We used a recording from a single turbine to prevent a nonrealistically varying acoustic stimulus caused by merging recordings from different sources and recording sites. The only difference from the original sounds is that it did not include infrasound, which was not the focus of this study and is below the hearing range of songbirds (Dooling, 2002; Dooling & Popper, 2007; Rogers et al., 2006). We broadcast the noise for the typical operation duration of wind turbines in the region based on wind speed from 1 to 1.5 h before sunrise (landing time of migratory birds [Chernetsov & Mukhin, 2006]) until 1 h after sunset. This range covers the resting and refueling hours of migrants as well as the foraging time of local birds. We placed the phantom turbine on a hilltop with the speaker positioned facing north-northeast (30°; calculated wind direction) because sound propagates from wind turbines such that most of the sound energy is directed downwind (Rogers et al., 2006). Wind direction was calculated as the median wind direction during daylight hours in the previous season. The speaker was placed 2 m off the ground, above the main vegetation level, allowing unobstructed sound propagation. During the before and after phases, we placed a dummy speaker at the same location.

Acoustic monitoring

We recorded the acoustic environment continuously during each experimental repeat in MP3 format at a sampling rate of 48 kHz and at a bit rate of 128 kbps at 12 locations with calibrated acoustic recording units (Roland R05 audio recorder) (Mennitt & Fristrup, 2012). This setting allowed us to measure absolute background sound levels instead of relative measurements. We deployed the recorders inside a fabric windscreen in Palestine oak (*Quercus calliprinos*) stands 1.5 m above the ground at varying angles and distances from the phantom turbine (0°, 90°, 180°, and 270°; 5, 70, 140, and 280 m) (Figure 1b).

We measured SPL in A-weighted decibels suited for human-related sound measurements and relevant for songbirds that have a similar hearing curve (Dooling & Popper, 2007). To describe the wind turbine noise, we used the hourly L_{50} (median noise exceedance level in dBA SPL), which is suited to describe continuous sources of noise, which we determined with custom programs (Damon Joyce, NPS, AUDIO2NVSPL, and Acoustic Monitoring Toolbox).

To account for the noise measurements' artifacts created by strong winds, we calculated Cook's (1977) distance to identify outliers of wind speed's effect on sound level (L_{50}) during daytime when wind turbine noise was not played. Wind speeds of 8 m/s or higher produced >10% outliers and consequently we removed noise measurements obtained at these wind speeds from all experimental phases. We acknowledge that this removed data that corresponded to conditions when turbines would be operating in the landscape, but because we expected greater impacts with increasing sound levels, it means our approach was conservative.

Measuring the effects of noise on songbirds

To measure the impact of the noise treatment on the songbird community, we conducted bird-ringing sessions on the second day of each experimental phase. Each session included 12 mist nets 12 m long and 2 mist nets 18 m long at fixed locations set 45 min before sunrise and left open for 4.5 h (hereafter bird-ringing hours [Appendix S5]). The nets were inspected every 60 min, except for rare cases of strong wind or high temperatures, when we inspected the nets every 30 min and summed every two extractions. The nets were placed at a gradient of distances (20–120 m) and at varying angles from the phantom wind turbine. We divided the capture area into four triangular slices and placed four nets in each slice (but only two at the upwind slice)—two close and two far. By doing so, we aimed to minimize bias in the setting while factoring in the heterogenous natural study site (with all the benefits of conducting a field experiment). Additionally, the nets were placed upwind, downwind, and perpendicular to wind direction (covering <180 degrees) rather than in a complete circle around the phantom wind turbine because we assumed noise propagated to both sides would be similar (as supported by the continuous sound measurements [Figure 1b]) and to assure birds' safety (by keeping the distance between the nets relatively short and thus reducing the time the birds spent in the nets).

None of the songbird species on site occur in flocks (Shirihai et al., 1996); thus, we assumed their movements were made at the individual level. For each captured individual, we collected date and time of capture, net location, species identity, age, and sex (when possible based on plumage differences), maximum wing chord and tail length (0.5 mm accuracy), and body mass (0.1 g accuracy). Species identification allowed the categorization of birds as migrant or nonmigrant; there were no species with both migratory and nonmigratory populations at this site at the time of study. All birds were released at the study site shortly after their capture. To avoid pseudoreplication and to minimize the inclusion of data from individuals who experienced repeated exposure to the noise treatment (Harding et al., 2019), all recaptured birds were excluded from the analyses (only first-capture data were used). All birds were handled following the national ethical guidelines (Israeli Nature and Parks Authority bird ringing permit A-302 and research permit 2018/41922).

Data analyses

We analyzed the data with R 3.4.4 (R Core Team (2022) in RStudio (RStudio Team 2022) with packages lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017). We used generalized linear mixed effects models (GLMMs) to test the effect of the experimental phase (before, noise treatment, and after as categorical variables; before phase reference condition) on different response variables. Appendix S6 contains the full list of models we used to analyze our data. We used Poisson distribution for abundance (total number), age, and sex, gamma distribution for species diversity (calculated as Fisher's alpha), and binomial distribution for the ratio of migratory to nonmigratory individuals and species. All models included the experimental repeat number (1–6, the repeated measures) as a random factor to account for possible temporal variation in the bird community and habitat throughout the season and for biases that may be caused by overdispersion in the Poisson models (Harrison, 2014). First, each model was compared with a null model that included only the random factor (i.e., experimental repeat). Second, using a likelihood ratio test (Alday, 2016; Zuur et al., 2009), we determined whether the insertion of the experimental phase factor significantly improved the model compared with the null model. Finally, for models that were significantly better than the null model, we calculated *p* values for each experimental phase.

For the three most abundant species in the area (see below), we separately tested the effects of the experimental phase on each response variable. If the experimental phase significantly affected categorical internal-state factors (i.e., age or sex group), we built separate models for each group (i.e., juveniles and adults, females and males) with Poisson distribution and followed the abovementioned process to explore specifically whether and how each group was affected by the noise treatment. We had six repeats for each experimental phase. For lesser whitethroats (*Sylvia curruca*), we used only the first four experimental repeats because none were caught during the last two experimental repeats.

Finally, we constructed a model to examine the spatial distribution of the noise impact. To do so, we used the daily number of birds captured at each net, correcting the number of captured birds at the two 18-m nets by dividing the number captured by 1.5 and rounding to the nearest whole number, which allowed the use of Poisson distribution. This model included the following explanatory variables: experimental phase, distance from the phantom wind turbine (in meters), direction from phantom wind turbine downwind axis (i.e., sound propagation direction in degrees), interaction among these three factors, and experimental repeat number as a random factor. Distance and direction were scaled and centered. We did not use sound levels directly as a predictor of bird abundance at each net due to the relatively sparse distribution of recorders compared with mist nets (Figure 1). S6

RESULTS

Acoustic monitoring

After removing 27.5% of all recorded data due to wind speed exceeding 8 m/s (see "Methods"), we were left with 1337 hourly values collected during the bird-ringing hours (Appendix S7). Specifically, we collected 85–127 hourly L_{50} sound level measurements over 21–28 days at each of the 12 recorders.

The sound level of the acoustic environment was similar at all locations during the before and after phases (except for

TABLE 1 Results of the generalized linear mixed effects model of the effects of wind turbine noise on bird abundance.[a]

Experimental phase and variable	Exp(estimate)	Estimate	SE	z (p)
Intercept including the before phase				
intercept[b]	38.99	3.66	0.16	23.49 (<0.001)
treatment phase noise treatment[b]	0.69	−0.38	0.1	−3.8 (<0.001)
treatment phase after	0.94	−0.06	0.09	−0.64 (0.52)
Intercept including the after phase:				
intercept[b]	36.79	3.61	0.16	23 (<0.001)
treatment phase noise treatment[b]	0.73	−0.32	0.1	−3.18 (<0.001)
treatment phase before	1.06	0.06	0.09	0.64 (0.52)

[a]Three experimental phases were compared: before, during noise treatment, and after wind turbine noise broadcast. Bird abundance is daily number of birds caught. The model also included the experimental repeat number (1–6) as a random factor to account for possible temporal variation in the bird community and habitat throughout the season and for biases that may be caused by overdispersion in the Poisson model. The model was structured as follows: daily bird number ~ treatment phase + experimental repeat number (random factor) (error distribution: Poisson. link function: log).
[b]Variable significantly affected bird abundance.

the relatively high values from the location bird-ringing side 140 m, which was more exposed to wind and the nearby road [Appendix S4]). At 11 of the 12 recording locations during the noise treatment, sound levels were considerably higher than before or after the treatment (Appendix S5). Altogether, the distribution of change in sound levels resulted from a combination of distance and direction from the phantom wind turbine (Figure 1b). The mean L_{50} sound level was higher during noise-treatment phase than before phase in all directions but not at all distances.

Abundance and distribution

We caught and ringed 670 birds (652 new and 18 recaptured from previous ringing days that were removed from the data analyses; see "Methods") of 26 different species (Appendix S2). The three most common species were all in the *Sylviidae family* (warblers). The noise significantly reduced the number of birds we sampled daily, including lowering the abundance of two of the three *Sylviidae* species. This reduction in bird abundance had a distinct spatial pattern.

Mean daily number of songbirds caught showed a significant decline of approximately 30% during the noise treatment compared with the before and after phases (before 41.33 [SE 7.58]; noise treatment 28.33 [5.35]; after 39.0 [4.95]; likelihood ratio test, $\chi^2 = 16.54$, df = 1, p<0.0003) (Table 1 & Figure 2).

The spatial model showed an impact of noise treatment on the daily number of captured birds. There was a significant interaction among treatment phase, distance from the phantom turbine, and direction. More birds were displaced from areas close to and downwind of the phantom wind turbine than from other areas. This pattern was significant for the noise-treatment phase and for the after phase. The effect was smaller for the after phase (likelihood ratio test, $\chi^2 = 23.35$, df = 7, p<0.001) (Table 2 & Figure 1c).
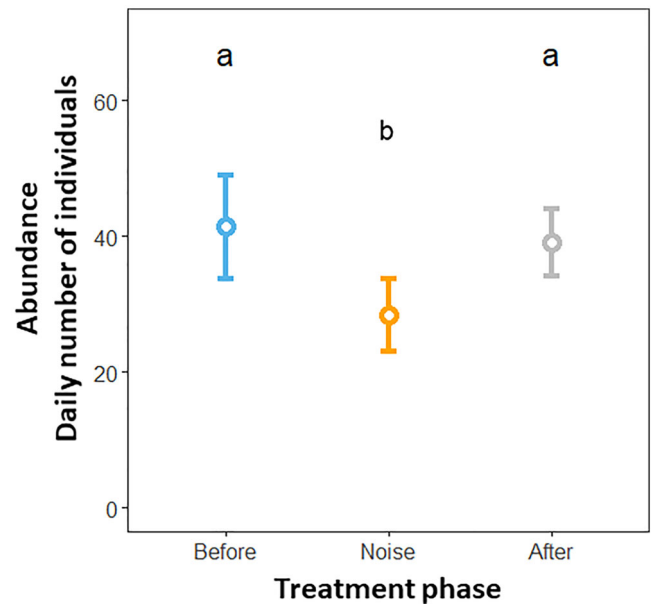

FIGURE 2 Daily number of individuals of all songbird species across experimental wind turbine noise treatment phases before, during noise treatment, and after wind turbine noise broadcast (circle, mean; vertical lines, SE; different letters, significant difference [p<0.001] [see statistical model in Table 1]). Each phase lasted 48 h and the entire experiment was repeated six times during the fall (postbreeding and migration) season.

Species composition

Although we found a small reduction in the number of sampled species with Fisher's α measure of biodiversity for the noise-treatment phase, this reduction was not significant (before mean [SE] = 3.14 [0.52]; noise treatment: 2.77 [0.68]; after 3.5 [0.67]; likelihood ratio test, $\chi^2 = 2.91$, df = 1, $p = 0.23$). Altogether, 21 out of 26 species were migratory (Appendix S2). The ratio of migratory and nonmigratory species did not change during

TABLE 2   Results of the generalized linear mixed effects model of the effects of wind turbine noise on bird abundance and spatial distribution.[a]

	Exp(estimate)	Estimate	SE	z (p)
Intercept	2.37	0.86	0.15	5.6 (<0.001)
Before	1.08	0.08	0.1	0.83 (0.41)
Noise treatment[b]	0.70	−0.36	0.11	−3.22 (<0.01)
Direction	1.00	0	0.07	−0.06 (0.95)
Distance[b]	1.16	0.15	0.07	2.16 (0.03)
Before:distance	0.94	−0.06	0.1	−0.62 (0.53)
Noise treatment:distance	1.16	0.15	0.11	1.32 (0.19)
Before:direction	0.96	−0.04	0.1	−0.46 (0.65)
Noise treatment:direction	1.10	0.1	0.11	0.87 (0.38)
Before:distance:direction	0.90	−0.1	0.07	−1.6 (0.11)
Noise treatment:distance:direction[b]	0.77	−0.27	0.08	−3.43 (<0.001)
After:distance:direction[b]	0.85	−0.16	0.07	−2.35 (0.02)

[a]Three experimental phases were compared: before, during noise treatment, and after wind turbine noise broadcast. Bird abundance is daily number of birds caught. We also included in the model distance (m) and direction (deg) from the phantom wind turbine, their interactions with treatment phase (before, noise treatment, or after) and the three-way interaction between distance, direction, and treatment phase. In the two-way interactions, the noise treatment and before phases were each compared with the intercept (after phase and its interactions with distance and direction). The model also included the experimental repeat number (1–6) as a random factor to account for possible temporal variation in the bird community and habitat throughout the season and for biases that may be caused by overdispersion in the Poisson model. The model was structured as follows: daily birds number ~ treatment phase:distance:direction—distance:direction + experimental repeat number (random factor) (error distribution: Poisson. link function: log). Colons represent interactions.
[b]Variable significantly affected bird abundance.

noise treatment compared with before or after phases (likelihood ratio test, $\chi^2 = 0.2$, df = 2, $p = 0.91$). Moreover, we found no difference in the reaction of individuals of migratory species and individuals of nonmigratory species to the noise treatment as implied by the constant ratio between the numbers of caught individuals from the two species groups. Approximately 70% of captured individual birds were migratory and 30% were nonmigratory regardless of experimental phase (before 0.68 [0.05]; noise treatment 0.70 [0.03]; after 0.70 [0.03]; likelihood ratio test, $\chi^2 = 0.17$, df = 1, $p = 0.92$). Similarly, the noise treatment did not have a significant impact on the ratio of individuals from migratory and nonmigratory species when excluding the three most common *Sylvia* species (likelihood ratio test, $\chi^2 = 1.72$, df = 2, $p = 0.42$).

Population-level responses of Sylvia warblers

Eurasian blackcap (*Sylvia atricapilla*), lesser whitethroat (*S. curruca*) (both migratory), and Sardinian warbler (*S. melanocephala momus*) (nonmigratory) were the most common species caught (over 100 sampled individuals for each species) (Appendix S3). We identified the age of most blackcap and lesser whitethroat individuals (97.4% and 99.2%, respectively) but only of two-thirds of Sardinian warblers (66.9%) (Appendix S8). We visually identified the sex of 258 blackcap and Sardinian warblers, representing 99.5% and 99.4% of the individuals from each species, respectively (Appendix S9). The extensive data for these species allowed us to further examine the effects of the noise treatment on them.

The noise treatment affected each species differently (Figure 3). For the lesser whitethroat, the decline in abundance

(i.e., daily mean number of individuals) was consistent during the noise treatment and the after phases when compared with the before phase (mean before 13.25 [SE 6.99]; noise treatment 8.5 [2.99]; after 8.0 [1.96]; likelihood ratio test, $\chi^2 = 6.49$, df = 2, $p < 0.05$) (Appendix S10 & Figure 3a). Similarly, for the Sardinian warbler, we found a significant decline during the noise treatment when compared with the before phase, but the after phase was not significantly different from either of the other phases (before 11.0 [2.41]; noise treatment 6.0 [1.65]; after 8.17 [1.8]; likelihood ratio test, $\chi^2 = 9.01$, df = 1, $p < 0.02$) (Appendix S11 & Figure 3b). The effect of the noise treatment was not significant for the blackcap compared with the before and the after phases (before 10.83 [2.95]; noise treatment 9.0 [2.11]; after 11.67 [3.13]; likelihood ratio test, $\chi^2 = 2.17$, df = 1, $p = 0.34$) (Figure 3c).

For the lesser whitethroat only, we found a significant difference in the reaction of different age groups to the noise treatment; the ratio of juveniles to adults was lower for noise and after phases compared with before (mean before 0.81 [SE 0.11]; noise treatment 0.53 [0.17]; after 0.62 [0.11]; likelihood ratio test, $\chi^2 = 6.61$, df = 2, $p = 0.04$). This occurred because fewer juvenile individuals were found at the site during the noise treatment and the after phases compared with the before phase (before 9.75 [4.33]; noise treatment 3.75 [1.38]; after 5.25 [1.44]; likelihood ratio test, $\chi^2 = 12.04$, df = 2, $p < 0.005$) (Appendices S8 & S12; Figure 4a). This trend was not observed in adult lesser whitethroats, which showed no significant change in daily number in relation to the experimental phase (before 3.5 [2.87]; noise treatment 4.5 [2.33]; after 2.75 [0.85]; likelihood ratio test, $\chi^2 = 1.72$, df = 1, $p = 0.42$) (Appendix S8 & Figure 4b). We did not find age effects for blackcaps or Sardinian warblers. Also, in both species where sex can be visually identified (blackcap
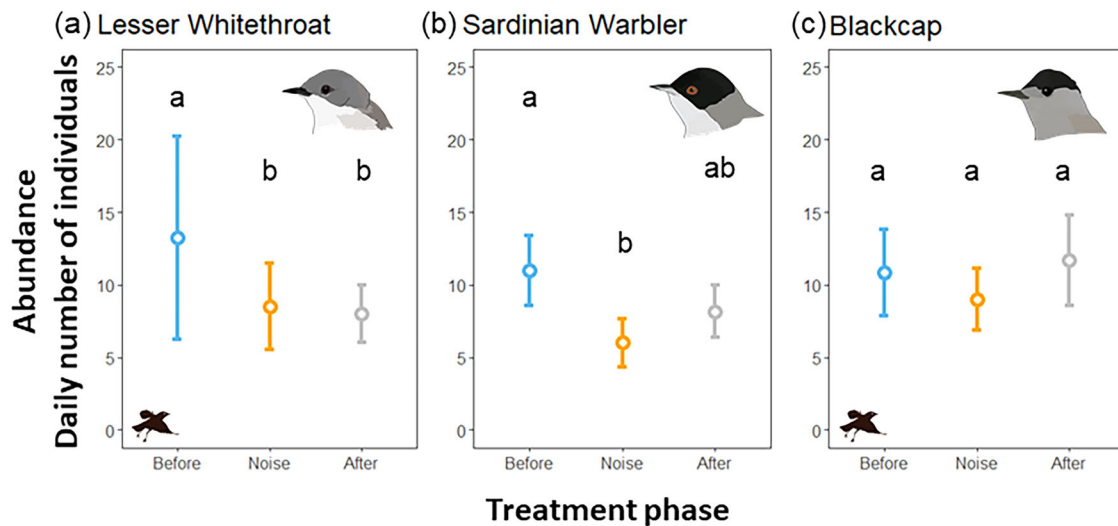
FIGURE 3 Daily number of individuals of S*ylvia* warblers before, during noise treatment, and after wind turbine noise broadcast: (a) lesser whitethroat (*Sylvia curruca*) (migratory), (b) Sardinian warbler (*S. melanocephala momus*) (nonmigratory), and (c) Eurasian blackcap (*S. atricapilla*) (migratory) (circle, mean; vertical lines, SE; different letters above bars, significant differences for each species [*p*<0.05] [see statistical models in Appendices S10 & S11]; flying bird icon, migratory species).
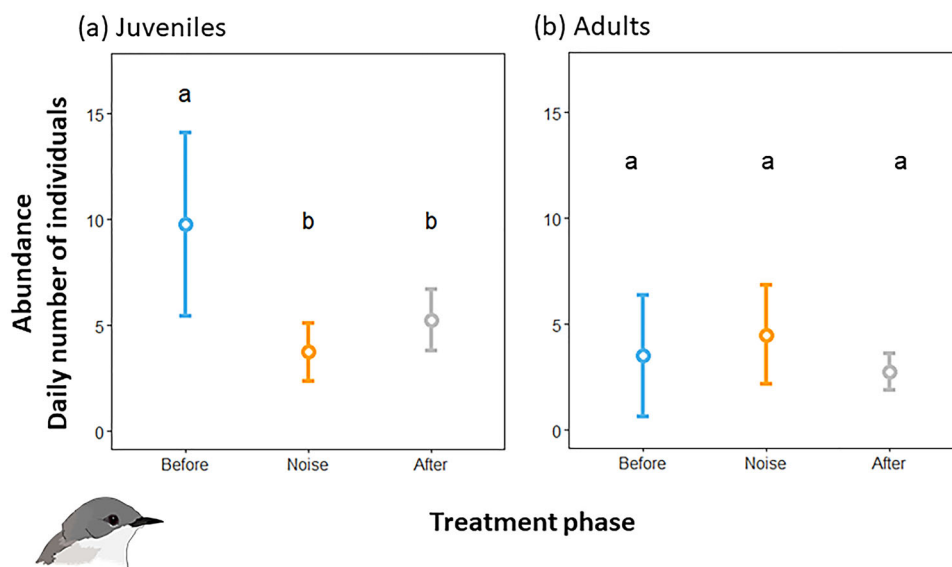

FIGURE 4 Abundance of (a) juvenile and (b) adult lesser whitethroats (*Sylvia curruca*) measured as their daily number across experimental wind turbine noise treatment phases: before, during noise treatment, and after wind turbine noise broadcast (Appendix S8) (circle, mean; vertical lines, SE; different letters, significant difference for each age group [*p*<0.05] [see statistical model in Appendix S12]).

and Sardinian warbler), we found no significant effect of sex on reaction to noise.

DISCUSSION

Our results showed a direct and strong negative impact of wind turbine noise on songbirds. By broadcasting wind turbine noise, we were able to isolate the impact of noise from other possible effects of wind turbines and found an approx-

imate 30% decline in mean daily bird abundance during noise broadcast. This decline had a distinct spatial pattern: displacement was stronger for birds from areas closer and downwind of the phantom wind turbine. Individuals of migratory and nonmigratory species reacted to the change in the acoustic environment in a similar fashion. Correspondingly, the noise treatment did not cause a significant change in species composition. Nevertheless, we found a substantial reduction in the daily abundance of two of the three most common species we examined.

Acoustic environment

We quantified sound levels of the experimentally manipulated acoustic environment while measuring changes in the bird community and population structure to better understand the relations between anthropogenic noise pollution and its ecological consequences (Lehnardt et al., 2019; McKenna et al., 2016; Shannon et al., 2016). Specifically, noise generated by wind turbines has a typical spatial propagation pattern according to the wind direction and speed (Dai et al., 2015). Here, the measured sound levels from the phantom wind turbine fit the general expectations from an operating wind turbine: during the noise-treatment phase, sound levels increased throughout the study site in all directions around the phantom wind turbine. The highest sound levels were measured downwind and the lowest upwind from the phantom wind turbine, and there was a gradual reduction in the level of noise from the center outward (Figure 1b). This result strongly supports the validity of this method, allowing future researchers to continue distinguishing noise effects from other confounding effects generated by wind turbines, as was previously done for roads (McClure et al., 2013) and natural gas fields (Cinto Mejia et al., 2019). However, specific wind turbine models placed at particular sites may produce different noise levels at the distances we used (Dai et al., 2015). In addition, the noise propagation of real wind turbines is expected to reach much farther than our speaker due to their substantially greater size and height above the ground. At a larger scale, sound levels from entire windfarms can be modeled for specific sites to allow for a realistic impact evaluation (Sun et al. 2018). Accordingly, when using our data for wind infrastructure planning, it is vital to extrapolate the expected sound levels for the planned windfarm's specific circumstances and spatial distribution. This procedure will ensure better precision of models and ecological impact assessments when developing windfarms in remote or nonurban, open landscapes.

Overall, the experimentally broadcasted wind turbine noise strongly affected the natural acoustic environment, increasing the sound levels by up to 60 dBA (Figure 1b). In this respect, it is important to realize that although environmental impact assessments often consider a change of a few decibels as having a negligible impact, a change of 3 dBA already reduces the hearing range of birds by half, a change of 6 dBA reduces the hearing range by three-quarters, and a change >12dBA reduces the hearing range of a bird by more than 90% (Barber et al., 2010). This means that at the core of the wind turbine noise-polluted area, which covers several hundred square meters, birds are expected to barely perceive any acoustic cues in their environment (within the frequency band of the noise). This limited ability to sense acoustic signals and cues may elicit various behavioral responses, such as avoidance behavior, reduced feeding rate, elevated antipredator behavior, and impaired communication (Barber et al., 2010; Francis & Barber, 2013; Shannon et al., 2016). In addition to the masking of acoustic cues, noise pollution may also distract exposed birds, reducing their ability to efficiently use the habitat (Dominoni et al., 2020). Lastly, exposure to noise pollu-

tion might negatively affect (directly or through complementary mechanisms) many physiological processes and lead to high-stress hormone levels, accelerated DNA damage, and reduced sleep quality, immune response, cognitive ability, and fertility (Kight & Swaddle, 2011).

Bird abundance and distribution

We found a decrease of ∼30% in the mean daily abundance of songbirds when broadcasting wind turbine noise. Similar rates of displacement in birds were found in previous studies with other sources of anthropogenic noise pollution, such as roadway traffic (McClure et al., 2013; Senzaki et al., 2020b; Ware et al., 2015) and natural gas extraction (Cinto Mejia et al., 2019), despite major differences in the studied species, habitat, and source of noise. Two out of the three most common species in our study showed an even greater rate of decline: 45% and 36% reduction in abundance of lesser whitethroats and Sardinian warblers, respectively. Despite the existence of extensive literature on wind turbine noise in terrestrial environments, we found no study in which the impact of such noise on bird habitat selection was examined. Notwithstanding, our findings contradict the claim raised by May et al. (2017) in their comprehensive review of offshore wind turbine–wildlife interactions that wind turbine noise will likely cause no displacement in birds, although the impacts of offshore and onshore turbines are not necessarily comparable. Ultimately, although the habitats surrounding wind turbines may seem to remain intact, they are no longer suitable for some birds because of an invisible pollutant: noise.

As mentioned above, each of the three focal species in our study reacted differently to the added wind turbine noise, despite having a similar life history (e.g., habitat preferences, diet, vocalizations [Shirihai, 2001]). While a better understanding of how these species interact with the acoustic niche during the postbreeding season is needed to explain the differences in their responses, it is worth noting that this result aligns with previous studies on the variation among displaced birds from noisy areas in general (Cinto Mejia et al., 2019; McClure et al., 2013; Ware et al., 2015) and windfarms in particular (without specific emphasis on noise [Fernández-Bellon et al., 2019; May, 2015; Percival, 2005; Stevens et al., 2013]). This result also stresses the need to identify noise-sensitive species of conservation concern and use of this knowledge to define habitats that are more vulnerable to noise pollution.

Inherently, the meaning of the decrease in bird abundance is that wind turbine noise reduces available habitat for many birds. Our results, therefore, are consistent with the findings of studies that highlight the role of wind turbines in causing habitat loss and fragmentation (Fernández-Bellon et al., 2019; Marques et al., 2019) and suggest that at least to some extent, the observed displacement found in windfarms is caused by noise. This rate of displacement occurs in addition to the hazardous effects of other factors, such as wake effects, pulsing lights, or others (Lovich & Ennen, 2013; Sun et al., 2018). Specifically, our results are in agreement with the results of Leddy

et al. (1999) and Stevens et al. (2013) on the impacts of wind turbines on grassland songbirds and the results of Fernández-Bellon et al. (2019) on forest songbirds. We found the same clear displacement gradient at similar distance ranges (several dozens to a couple hundred meters). Upscaling the impacts of a single wind turbine to entire windfarms, especially given their rapidly increasing global distribution (He & Li, 2020), points to a large-scale source of functional habitat loss and fragmentation worldwide. Because a primary driver of this fragmentation, noise pollution, is invisible, the risk of it being overlooked by landscape-centered fragmentation metrics is high (Berger-Tal & Saltz, 2019). Importantly, this impact is especially troubling given the fact that wind turbines are usually placed away from human settlements or other infrastructures, pushing windfarms to natural sites with minimal anthropogenic noise pollution. We strongly recommend that the impacts of noise pollution on wildlife be included in ecological impact assessments for wind power infrastructure. Moreover, the predictable spatial pattern of wind turbine noise (Katinas et al., 2016; Rogers et al., 2006) may allow for the mitigation of its impacts through proper planning and placement of turbines.

The open question is what causes the reduction in the number of captured birds during our noise broadcasts? Do birds leave the noisy area altogether or are they just less active and, therefore, less likely to be captured in mist nets? We suggest that for the most part, our results are due to habitat avoidance and displacement. Thanks to the setting of the experiment, it was evident that the number of the migratory lesser whitethroats remained low also in the last phase, after the noise treatment ended. Additionally, there were significantly fewer juveniles during and after experimental noise exposure compared with their rate before it. These findings support the notion that the population of lesser whitethroats was altered by the broadcast of wind turbine noise and did not shift back to baseline because the birds had left the site. Our finding that the abundance of nonmigratory Sardinian warblers only partially recovered after the noise exposure also supports this argument. We suggest that the displaced lesser whitethroats, a migratory species, moved farther away (to other stopover sites or continued migrating), whereas the displaced Sardinian warblers stayed close-by and returned more quickly to the site after the noise receded. Future studies should further test the underlying mechanism of the reduced numbers of observed birds, for example, by using innovative tracking devices (Taylor et al., 2017; Toledo et al., 2014).

Species composition and population-level responses

In contrast to previous studies on the effects of noise pollution on songbird communities (Francis et al., 2009; McClure et al., 2013; Senzaki et al., 2020b), we found no significant change in songbird species diversity. However, when examining the response rate in the three most common species, all *Sylvia* warblers, we found a clear difference among them; only two out

of three species showed a reduction in abundance due to noise. This implies that the lack of significant change in community structure in our study might result from a small sample size of species (the abovementioned studies had more than 40 species, whereas we had 26) or individuals. Surprisingly, previous studies on the effects of wind turbines on songbirds did not test for changes in community structure (but see Leddy et al., 1999 and Villegas-Patraca et al., 2012). Therefore, we recommend that further work be done to determine whether wind turbine noise causes changes in songbird species composition to be able to provide valid conservation recommendations.

In the lesser whitethroat, the response to noise depended on the age of the bird. There was a distinct reduction in the number of juveniles during and after noise exposure but with no significant change in the abundance of adults. This finding stands in contrast to many studies on bird populations that show that less experienced individuals normally stay in disrupted or lesser-quality habitats during migration or right upon arrival to the breeding ground (Habib et al., 2007; McClure et al., 2017; Yong et al., 1998). This result perhaps reflects a higher tendency of juveniles to move when redistributing at stopover sites (Chernetsov, 2006), in this case, in response to noise pollution. Nonetheless, it is yet to be tested whether inexperienced juveniles are less capable of withstanding the cost of noise compared with adult individuals and, therefore, make the effort to avoid the noisy habitat.

Klingbeil et al. (2020) tested the effects of anthropogenic noise pollution on 322 bird species and found that noise shapes the breeding distribution of migratory species to a similar extent as nonmigratory species. However, the effects of noise on migrants during their migratory journey were not tested. We found no difference among migrants and nonmigrants in their response to wind turbine noise. Furthermore, of the two focal species whose numbers significantly decreased during the noise broadcast, one was migratory and the other nonmigratory. This result contradicts our expectation that migrants will show a higher rate of avoidance during migration, based on greater reliance on acoustic communication or on acoustic environmental cues in a novel environment (Berger-Tal et al., 2014) or on their state of mobility (McClure et al., 2013). This result may be at least partially explained by the fact that nonmigratory species during the postbreeding season do not defend territories and roam locally, which means that migrants and nonmigrants during this time are not fully familiar with their surroundings or have a similar state of mobility. Importantly, despite a similar degree of reaction to noise between migratory and nonmigratory species, the decline in the number of migrants is especially alarming. Migratory bird populations are globally declining faster than nonmigratory birds, with notable declines in populations migrating to East Africa (Laaksonen & Lehikoinen, 2013; Sanderson et al., 2006; Vickery et al., 2023), as are the populations examined in this study. This decline is partly because of habitat quality degradation at stopover sites (Sillett & Holmes, 2002). Our results demonstrate that by degrading habitat quality, anthropogenic noise can be a key factor threatening migrating birds.

Study limitations

Although we addressed an important knowledge gap, it is essential to acknowledge our study's limitations. First, the study was conducted at a single site with a specific habitat type and a limited number of songbird species, thereby the generalizability of the findings is restricted. Additionally, we broadcasted a recording from a single turbine. It is recommended to use multiple recordings and replicate them several times (Kroodsma et al., 2001), but we faced a lack of high-quality recordings from various turbine models and wanted to avoid unnaturally varying stimuli. Moreover, the short duration of the postbreeding season limited us to only six repetitions, a low number that is suitable for statistical analyses for a single site and recording (based on expected residual variance values). Hence, we chose to repeatedly examine the response to a single recording at a single site. Furthermore, the study was conducted within a single year, overlooking potential interannual variation that could affect the observed outcomes. These limitations do not invalidate our results, but they constrain their generalizability and emphasize the need for further research to better evaluate the ecological impacts of wind turbine noise in other conditions.

Concluding remarks

The impact of noise pollution on wildlife is rarely considered in environmental impact assessments for most types of infrastructures and especially for wind turbines (Teff-Seker et al. 2022). Despite the remaining knowledge gaps, decision makers can rely on existing mapping tools, sound propagation models, and the vast noise pollution scientific literature to minimize hazardous impacts of wind turbine noise on biodiversity. Our results stress the need to consider these noise impacts on the environment when planning windfarms or other noisy infrastructures. Doing so will help preserve stopover sites for migratory birds and assure the availability of habitats used by birds and wildlife in general.

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SUPPORTING INFORMATION

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