Is it safe for honey bee colonies to locate apiaries near wind turbines?

Julie Fourrier, Ophélie Fontaine, Maïlys Peter, Julien Vallon, Fabrice Allier, Benjamin Basso, Axel Decourtye

Entomologia Generalis
Published online September 2023

Is it safe for honey bee colonies to locate apiaries near wind turbines?

Julie Fourrier[1,2,*], Ophélie Fontaine[1,2], Maïlys Peter[3], Julien Vallon[1,2], Fabrice Allier[1,2], Benjamin Basso[2,4] and Axel Decourtye[1,2]

[1] ITSAP-Institut de l'Abeille, Site Agroparc, 84914, Avignon, France
[2] UMT PrADE, Avignon, France
[3] CNR, rue André Bonin, 69316, Lyon, France
[4] INRAE, Site Agroparc, 84914, Avignon, France
* Corresponding author: julie.fourrier@itsap.asso.fr

With 2 figures and 3 tables

Abstract: Wind energy is considered as one of the most promising renewable energy sources. However the growth in wind farms over the last few years raises questions about the possible effects on ecosystems. The widely documented impacts on birds and bats have garnered much attention. On the other hand, few studies exist concerning the impact on insects, and notably pollinators, despite the essential pollination services they provide for food production and plant biodiversity. We evaluated the effects of wind turbines on the honey bee via young mated queen egg-laying activity, colony weight gain, and bee behavior at the colony level, and on the homing ability of foragers at the individual level. Our results did not show an impact of wind turbines on forager mortality or on the reproductive caste during mating flights, nor an alteration of the orientation of foragers returning to the hive. We also did not observe a disruptive effect on the behavior, development or functioning of the colonies. Our results, under the described experimental conditions, reveal new information that would support an absence of impact of wind turbines on honey bee colonies.

Keywords: Apoidea; *Apis mellifera* L.; wind energy; queen egg laying; colony development; honeybee behaviour; homing flight

1 Introduction

Faced with the intensification of climate change and a growing global demand for electricity, renewable energies have increased in importance. Among those energies, wind energy has been rapidly developed since the 2000s and is on the horizon for 2050 as one of the most promising alternatives to fossil fuels (European Commission 2011). The European Union is a leading actor and accounted for 28% of the global wind power capacity with 236 Gigawatts in 2021 (WindEurope 2022; https://gwec.net/global-wind-report-2022/).

The establishment of terrestrial wind farms has led to the modification of land use and landscape characteristics, including agricultural areas. The development of wind energy thus raises the question as to its potential environmental impact on ecosystems. For flying fauna, much attention has been paid to the direct impact of wind turbines on birds and bats, by collision or barotrauma (tissue damage in bats due to sudden pressure changes near working turbine blades), as well as the indirect impact on habitat loss linked with disruption or avoidance of and movement away from the turbine area (Schuster et al. 2015, Marques et al. 2020, Leroux et al. 2022). Moreover other studies in birds or bats have looked at the attractive or repulsive effects of the noise or light detectors of wind turbines (Schuster et al. 2015, Zwart et al. 2016, Guest et al. 2022). In Europe, the feasibility of installing wind turbines on a site must take into account environmental impact studies on flora and fauna, in particular, birds and bats. The goal of these studies is to evaluate the effects and to propose measures in order to avoid, reduce, or even compensate for, the negative impacts (European Commission 2021).

The impact of wind turbines on flying invertebrates, such as insects, has, on the other hand, received less attention. The lethal effects of collision with wind turbines have been studied through insect carcasses and residues collected on the edges of the blades (Long et al. 2011, Voigt 2021) but groups or species potentially at risk and potential impact on populations are not currently known. Insects flying between 100 and 1200 m for migration or hilltopping, which refers to the congregation of insects at high altitudes (for example,

DOI: 10.1127/entomologia/2023/1858
E. Schweizerbart'sche Verlagsbuchhandlung, 70176 Stuttgart, Germany, www.schweizerbart.de

for courtship ritual), (Chapman et al. 2002) could interact with wind turbines (Voigt 2021, Guest et al. 2022). Insect collision could occur due to attraction to the color of, or light or heat emitted by the operating wind turbines (Guest et al. 2022, Long et al. 2011). Few studies have investigated the impact of wind farms on important groups like insect pollinators. One study by Pustkowiak et al. (2018) compared plant and pollinating insect species composition in three different areas of a managed homogeneous farmland landscape: areas around wind farms, grassland patches, and adjacent arable crops. They showed that species abundance and diversity around wind farms were similar to those found in grassland and were higher than in the adjacent crops. Insect pollinators provide an essential ecosystem service by pollinating wildflower plants and 75% of cultivated crop species, which represents an economic value of 153 billion Euros (Klein et al. 2007, Gallai et al. 2009). The current global decline of insects and wild pollinating species is worrying. The most often cited possible causes are bio-aggressors (parasites, pathogens, viruses), chemical contaminants, and habitat destruction associated with a reduction in floral resources (Osborne 2012).

No published study on the impact of wind turbines has focused on the managed honey bee. The honey bee is an economically important pollinator involved in the pollination of major crops and fruit production around the world as well as in honey production. Although not a declining species, environmental threats (e.g. reduction in floral resources, chemical contaminants) and economic difficulties adversely affect beekeeping. In central Europe, honey bee colony losses have been evaluated at 25% between 1985 and 2005 (Potts et al. 2010). The development of wind turbine activity on lands that are also used for beekeeping brings up the issue of the possible effects on bees and colonies. An initial hypothesis could be a direct, lethal effect of wind turbines on nearby individuals through collision or turbulence of the rotating blades. Another one, already proposed for birds, bats and even human health (Knopper et al. 2014), concerns the indirect impact on the colony due to the noise and vibrations generated by the blades of wind turbines. Intracolony communication includes the emission and perception of vibratory and sound signals (Kirchner 1993). These signals, emitted by dancing foragers and defined as the round dance for a close food resource within a few meters away and the waggle dance for a distant food source, transmit information to other bees about the direction (waggle dance), distance, and relative quality of the food resource in order to recruit nestmates for foraging (Kirchner 1993, Hunt & Richard 2013). This function is important to supply the colony with food resources. Worker honey bees can perceive sounds carried in the air at low frequencies from 10 up to 500 Hz (Kirchner et al. 1991, Kirchner 1993) and wind farms can emit sounds at a similar frequency range, between 20 and 200 Hz (Schmidt & Klokker 2014). Thus, some beekeepers (pers. comm.) suspect a problem of interference between the sounds and vibrations generated by the wind turbines and those used by the bees to communicate with negative consequences on the behavior, development and survival of the colonies. A final hypothesis concerns the disruption of the orientation of bees due to the flicker and strobe-like effects of the blade movement in sunny conditions or under the influence of the electromagnetic fields produced.

In this study, by comparing colonies at different distances from the turbines, we evaluated the potential impact of wind turbines on the key activities of the honey bee: i) at the colony level, on the egg-laying activity of young queens after they mate (reflecting mating success), on the weight gain and also on the aggressive behavior of the bees, and ii) at the individual level, on the homing ability of foragers that collect food resources, a skill that calls for cognitive capabilities and spatial orientation (Capaldi & Dyer 1999).

2 Material and methods

2.1 Experimental sites and bees

The study was conducted at two wind farm sites of the Compagnie National du Rhône (CNR) situated in Le Pouzin in the Ardèche region and Bollène in the Vaucluse region (France). These two sites are located next to a river (Rhône). The honey bee colonies used were hybrids resulting from cross-breeding between genetic strains of Buckfast bees with proper foraging activity and no visible disease symptoms as called for by published guidelines (OEPP/EPPO 2010).

For each of the two wind turbine sites, five apiaries made up of 10 to 14 colonies with virgin queens (a total of 59 and 70 colonies in Le Pouzin and Bollène, respectively) plus one colony with a mated queen were set up at different distances along the row of wind turbines. The virgin queens were introduced into the colonies at a maximum of 24 h before installation on the site. Two male (drone) hives were set up at the outer apiaries 1 and 5, at the ends of the row of wind turbines (Fig. 1). The colonies with the virgin queens and the colonies supplying the males, that were included to ensure the mating of queens in all apiaries, were set up with 6-frame hives and were used to assess mating success. The colonies with mated queens were used for the homing study and were set up in 10-frame Dadant hives.

The hives were brought to the sites on May 14 and 18 of 2020 for the sites in Le Pouzin and Bollène, respectively. The study was conducted in June and early July of 2020. During the study, the colonies were managed by experienced beekeepers.

2.2 Wind turbines

The wind turbines were the model Nordex N90 and consisted of an 80-meter-high tower and a 90-meter-diameter rotor with three 45-meter-long blades assembled in a helix. The site at Le Pouzin had two turbines spaced 520 m apart. The site at Bollène had three turbines spaced 430 m between

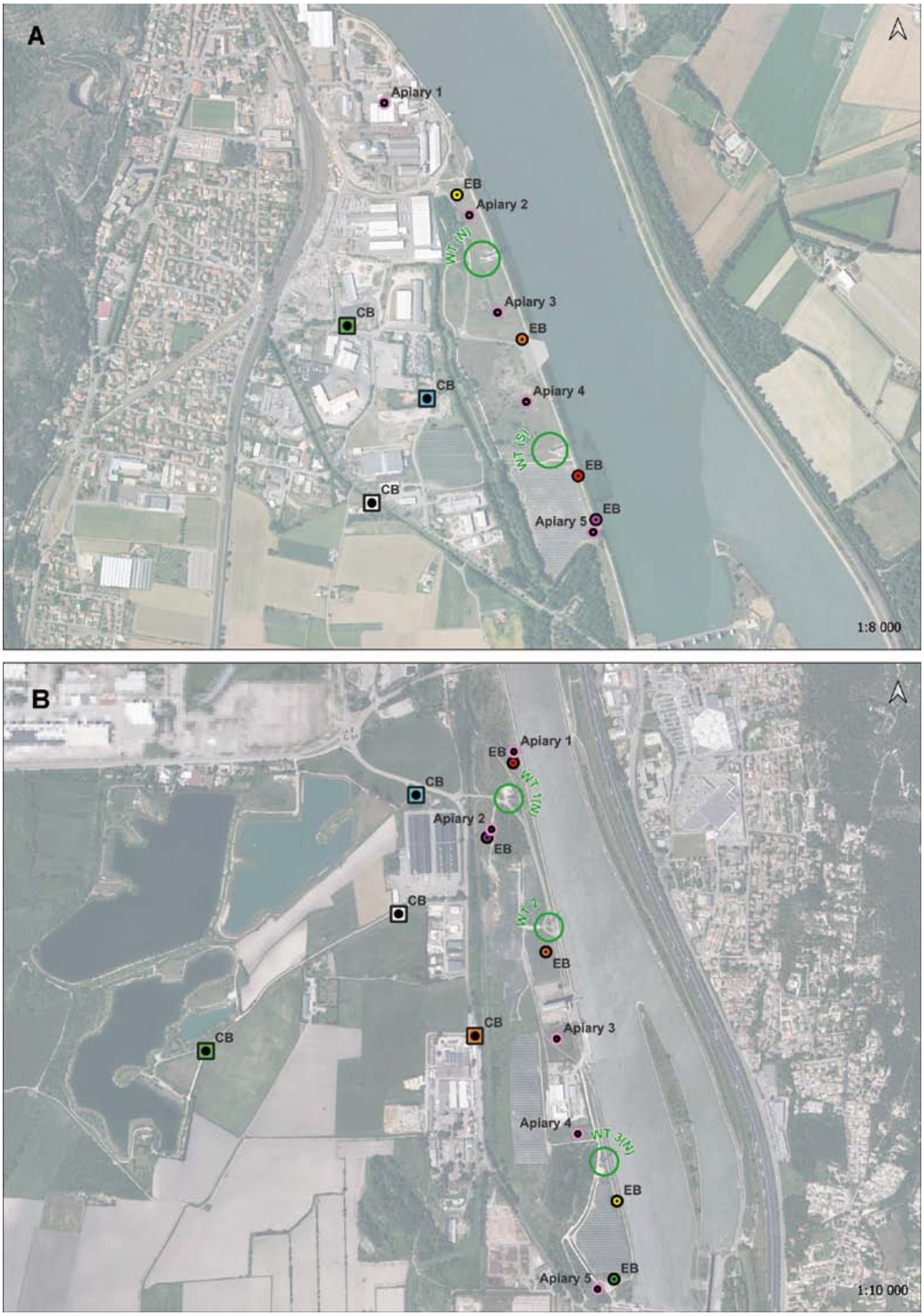

Fig. 1. Site cartography for **(A)** Le Pouzin and **(B)** Bollène with i) the localization of the apiaries 1 to 5 (pink points), each made up of 10 to 14 colonies with 6-frames (used for the experiments at the colony level) plus one 10-frame colony (used for the homing experiment on foragers), and the wind turbines ("WT") with green circles representing the footprint of 45 m corresponding to the radius of action of the blades, ii) the different release points choosen to intersect one or several turbine footprints (exposed bees "EB" represented by colored dots) and to not intersect any turbine footprints (control bees "CB" represented by colored squares) for the homing experiment. Same CB or EB release points were used to release the bees of different 10-frame colonies. In Le Pouzin, correspondence between the release points used and the colony/apiary number to which the released bees belonged to was: i) for CB: white square = 1, 2, 3, 4; blue square = 1, 5 and green square = 3, 4, 5; ii) for EB: orange dot = 1, 2, 5; red dot = 1, 2, 3; yellow dot = 3, 4, 5 and pink dot = 4. In Bollène, correspondence was: i) for CB: blue square = 1, 2, 3, 4; white square = 1, 2; salmon square = 3, 4 and green square = 1; ii) for EB: red dot = 1, 2, 3, 4; orange dot = 1, 2; yellow dot = 3, 4 and green dot = 1. Correspondence between colored symbols and groups of bees (EB and CB) released for each colony/apiary is detailed in Table S2.

the northernmost turbine (1) and that in the middle (2) and 790 m between turbine 2 and the southernmost turbine (3) (Fig. 1). Proper functioning of the wind turbines was assessed by comparing the energy effectively produced in a month (MWh) and during the study period (May to July 2020) to the expected production for Le Pouzin and Bollène wind farm sites (Table S1). During this overall period, Table S1 illustrates that wind turbine produced 112% and 94% of the expected energy to be produced at Le Pouzin and Bollène respectively. In this context, wind turbines of the two wind farms functioned normally, with a representative rotation of the blades for both sites.

2.3 Evaluation of egg-laying activity of queens

For the two wind farm sites, mating success of young queens was evaluated through the egg-laying activity 5 to 6 weeks after the establishment of the colonies with virgin queens (June 24 in Bollène and June 25 in Le Pouzin).

The number of frames with open brood (eggs and larvae) and capped brood (pupae) was noted and the food reserves (nectar/honey and pollen) were inspected. Mating failure was characterized by an absence of workers eggs during the hive inspections that led to a failure of colony development.

2.4 Evaluation of colony weight gain

For the two wind farm sites, the colonies were weighed using a mobile, electronic scale (Dini Argeo®) initially, 2 to 3 weeks after colony installation (June 2 in Le Pouzin and June 10 in Bollène) and then 5 to 6 weeks after colony installation (June 24 in Bollène and June 25 in Le Pouzin). The weight was recorded to determine the weight gain (kg) between the two observations. The evaluation of weight gain concerned only the colonies with egg-laying queens in order to compare development between apiaries.

2.5 Honey bee defensive behavior

In parallel to the first colony weight recording, defensive behavior was qualitatively evaluated by two trained operators using a scoring system (Costa et al. 2012). This method is commonly used in European breeding programmes. A note between 1 (nervous bees with strong defensive behaviour) and 4 (very gentle and calm bees) was attributed to bees of each colony. The bees were originally selected for calm and non-defensive behavior. The evaluation was performed 2 to 3 weeks after colony installation (June 2 in Le Pouzin and June 10 in Bollène) according to two criteria, i) gentleness and ii) calmness on the frame. The notation criteria were as follows:

1. i) The colony has a strong defensive reaction (stinging) and working without a lot of smoke and protective clothing is not possible; ii) bees nervously leave the combs, and cluster inside or outside the hive.
2. i) Much smoke and protective clothing are necessary to avoid stinging, ii) bees partly leave their combs and cluster on the edges of frames.
3. i) Colony can be handled without stinging if using a little smoke and no protective clothing is necessary, ii) bees are moving, but do not leave their combs during handling.
4. i) No use of smoke and no protective clothing are necessary to avoid stinging during the handling, ii) bees “stick” to their combs without any notable reaction to being handled.

2.6 Forager homing experiment

The bees of each 10-frame colony from the apiaries 1 to 5 in Le Pouzin (5 colonies) and the colony from the apiaries 1 to 4 in Bollène (4 colonies) were tested for the homing experiments (Fig. 1, Table S2). One homing test used the foragers from a single 10-frame colony in one apiary and foragers from two to three colonies were tested each experimental day (June 8 and June 9 in Le Pouzin; June 10 and July 4 in Bollène). The experiments were conducted with meteorological conditions favorable to both flight activity of foragers and the functioning of the wind turbines, which corresponded to wind speeds above 9 km/h (2.5 m/s) at the height of the wind turbine (to generate rotation of the blades) and temperatures greater or equal to 20°C (Tan et al. 2012) with average wind speeds of less than 20 km/h at the height of the released bees (optimal average wind speed for flight ≤ 15 km/h, Rollin et al. 2013). For the experiment on June 10, 2020 in Bollène, two of the three wind turbines were working. Wind turbine 1, the northernmost on the site, was not functioning due to maintenance.

The morning of the experiment between 120 and 140 foragers returning to the hive per colony were collected on the flight board and placed by groups of 40–45 bees in cages supplied ad libitum with a sugar paste (candy). The caged bees were transported under a large tent, sheltered from the wind and direct sunlight and were transferred one by one into a holding cage; a foam plunger allowed us to immobilize the bees without hurting them while they were each equipped with a metallic chip, of around 1 mg (± 1% of the bee’s weight) colored with Posca® marker according to the assigned treatment. The chips were glued to the thorax of the bees with dental cement (TempoSIL2, Coltène®). The bees were then transferred by groups of 15 into cages supplied with water and candy, with each cage corresponding to an assigned treatment group (turbine(s) intersected or not (control bees) for each distance of release from the colony, Fig. 1 and Table S2). Sixty to ninety bees per colony were tagged.

The cages with the labeled bees were next transported in the afternoon between 14:00 and 16:00 to release points corresponding to the assigned treatment to be released at around one meter above the ground.

The footprint of a wind turbine was determined by taking into account the vertical radius of action of the blades, which was 45 m (Fig. 1). The captured foragers from one 10-frame colony in one apiary were separated into two groups, called the control (CB) and exposed (EB) groups of bees that were released at the same time. The control bees (CB) were released at a spot such that the shortest theoretical trajectory between the release point and the hive did not intersect a wind turbine footprint. The release points for the exposed foragers (EB) were determined so that the shortest theoretical linear trajectory between the release point and their hive intersected the footprint of one or multiple wind turbines. For bees of the same 10-frame colony in one apiary, several release points located at different distances from the original colony were used to ensure that the exposed groups must intersect one, two or three (Bollène site) turbine footprints in a direct trajectory on returning to the hive (Fig. 1 and Table S2). To compare the performance of the control bees with those of the exposed bees, the distances between their release points and the colony were comparable (Table S2). Same EB or CB release points were used to release the bees of different 10-frame colonies (Table S2).

A magnetic bar system was set up at the entrance of each of the 10-frame hives in order to track the foragers of interest returning to the hive. The tagged bees became stuck to the magnet bar and were recorded every 5 minutes for 1 hour, and then at 2 hours after release. This 2-hour period is determinant for the homing of foragers as it was observed that a great majority of bees return to the hive two hours after release (up to 90% or more for bees familiar with the journey back to the colony, OECD 332, 2021). The great majority of bees freed themselves by leaving the metallic chip attached to the magnetic bar. Only a few bees needed to be freed by the observer. The chips were then collected and counted to assess the homing performances.

At the time of release, the local meteorological conditions for temperature (°C), hygrometry (%), wind speed (m/s) and direction, measured at about one meter above the ground (release height of the bees) were recorded with a portable thermo-hygrometer (Testo 174H®) and anemometer (Testo 410i®; Table S3). The conditions were representative of the time period at release and during the tracking of the homing of foragers (14:00–18:30). With the exception of wind turbine 1 that was being serviced during the experiment on June 10, 2020 in Bollène, the turbines were all working at the two sites during the release and tracking period (14:00–18:30). The wind speeds recorded at the height of the turbines (80 m) were largely above the minimum required of 2.5 m/s (or 9 km/h) for the turbines to function (Table S4).

2.7 Data analyses

The statistical analyses were conducted with the statistical software R version 3.6.1 (R Core Team 2019). To compare the egg-laying success of queens between the colonies of different apiaries, (presence of a laying queen or not), a Fisher's exact test ($P < 0.05$) was conducted on the recorded data 5 to 6 weeks after colony installation.

Weight gain of the colonies containing laying queens and bee defensive behavior (gentleness and calmness on the frame) were compared between apiaries with a non-parametric Kruskal-Wallis test ($P < 0.05$) due to the non-normal distribution (Shapiro test; $P < 0.05$).

The effect of exposure to wind turbines on the homing success of foragers was evaluated with generalized linear mixed models (GLMM) with a logit link function using the R package lme4 (Bates et al. 2022). The homing flight was treated as a binary response variable and coded as 1or 0 for each returning or non-returning bee respectively. To conform to the assumption of independent outcomes in the binary homing observations, the identity of the colonies tested was considered as a random variable. Exposure to wind turbines (passing by 0, 1, or 2 turbines in Le Pouzin and 0, 1, 2 or 3 turbines in Bollène) was included as a fixed explanatory variable. The other fixed explanatory variables considered in the analysis were the local temperature (°C) and wind speed (m/s), two variables that could have an effect on the flight activity and the homing of the bees (Henry et al. 2014, Rollin et al. 2013), and the shortest theoretical distance (m) between the release point of the bees and the colony. The distance and wind speed variables were log-10 transformed. The effects of explanatory variables, alone or in interaction with wind turbine exposure, on homing success were taken into account by considering a multi-model inference procedure (Burnham & Anderson 2002) using the R package MuMIn (Barton 2022). This procedure allows producing a single global model by averaging the coefficients of the explanatory variables within a set of simpler models, with respect to each model's relative weight of evidence. The weight of evidence ω_i of a simpler model i, based on the Akaike information criterion (AIC), gives the probability that model i is the best one in the model set, considering a parsimony trade-off between fit and complexity. The multi-model inference procedure was restricted to the sub-set of best models with a 95% cumulative weight of evidence that is with 95% chance of including the most parsimonious combination of explanatory variables. Averaged coefficients are computed along with the standard error, making it possible to derive P-values to assess the significance of each explanatory variable in the global model, based on its occurrence and relative contribution to the cumulative weight of evidence within the 95% best model sub-set. The relative importance ranges from 0 (variable absent from the best model subset) to 1 (variable present in all the best models), and increases when it occurs in models with greater weights of evidence.

Each explanatory variable was standardized beforehand to the range [0,1], which rendered variable values more readily interpretable in terms of effect and comparable to each other.

3 Results

3.1 Effects of wind turbines on egg-laying activity of queens

Five weeks (Le Pouzin) and six weeks (Bollène) after the installation of the colonies, the percentage of laying queens (successful mating) for all of the apiaries, was 77.97% in Le Pouzin (59 colonies) and 87.14% in Bollène (70 colonies). A single apiary in both Le Pouzin and in Bollène showed a lower rate at 63.6 and 64.3%, respectively, without being attributed to the impact of the turbines. The apiary concerned in Bollène was the furthest away from the turbines, but not the apiary in Le Pouzin (Table 1).

The results did not show significant differences in terms of egg-laying activity of queens between the apiaries located at different distances from the line of turbines (Table 1), for both Le Pouzin (Fisher exact test, $P = 0.605$) and Bollène sites (Fisher exact test, $P = 0.0945$).

3.2 Effects of wind turbines on weight gain of the colonies

Between the first and second observation dates, the weight gain of the colonies with laying queens reached a maximum of 6.20 kg for Le Pouzin and 7.40 kg for Bollène. The median weight gain varied between 2.90 kg (apiary 1) and 3.65 kg (apiary 3) in Le Pouzin and between 1.90 kg (apiary 2) and 3.40 kg (apiary 5) in Bollène (Fig. 2). For the two sites, the weight gain of the colonies did not significantly differ between the apiaries positioned at different distances from the row of wind turbines (Kruskal-Wallis $Chi^2 = 3.491$, df = 4, $P = 0.479$ for Le Pouzin; Kruskal-Wallis $Chi^2 = 3.527$, df = 4, $P = 0.474$ for Bollène).

3.3 Honey bee defensive behavior

For each of the sites studied, the bees exhibited gentle to very gentle behavior and were calm to immobile on the comb with average scores recorded by apiary between 3.6 and 4 in Le Pouzin and between 3.9 and 4 in Bollène (Table 2). Bee defensive behavior did not significantly differ between the apiaries at Le Pouzin (Kruskal-Wallis $Chi^2 = 4.747$, df = 4, $P = 0.314$ for gentleness; Kruskal-Wallis $Chi^2 = 6.300$, df = 4, $P = 0.178$ for calmness on the frame) and at Bollène (Kruskal-Wallis $Chi^2 = 2.503$, df = 4, $P = 0.644$ for gentleness; Kruskal-Wallis $Chi^2 = 3.659$, df = 4, $P = 0.454$ for calmness on the frame).

3.4 Effects of wind turbines on forager homing performance

For the experiment conducted in Le Pouzin, a total of 283 foragers tagged with a metallic chip were released. Two hours after the release of the foragers the overall homing success was at 75.0% (n = 140 bees released) for the control group and 78.3% (n = 143 bees released) for the treatment group.

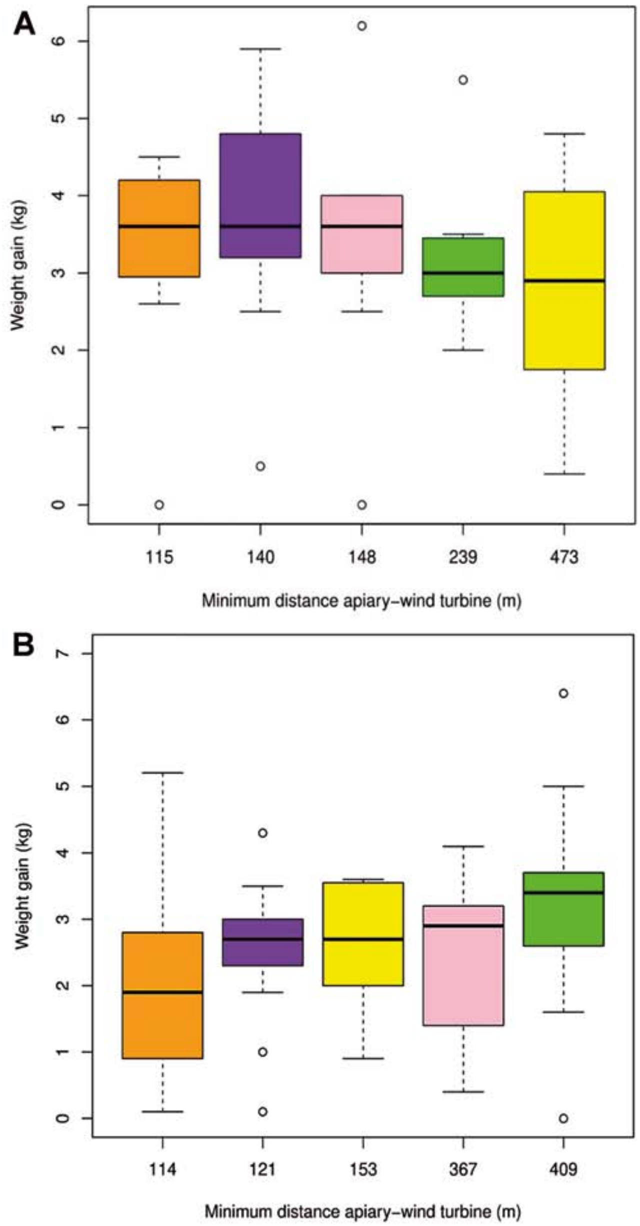

Fig. 2. Weight gain (kg) for the colonies of each apiary (medians, 1st and 3rd quartiles) according to their distance from the closest wind turbine for **(A)** Le Pouzin and **(B)** Bollène (yellow = apiary 1, orange = apiary 2, pink = apiary 3, purple = apiary 4, green = apiary 5).

The results of the GLMM did not show a significant negative effect on the foragers of intersecting the footprint of one or two turbines during their return back to the hive (Table 3). Other variables, like the release distance from the hive, the wind speed (m/s), the temperature at time of release (°C) or even the interaction of the factors of distance, temperature and wind speed with the number of turbines passed did not have a significant effect on the homing success of the bees.

Table 1. Queen egg-laying rate per apiary and site according to the distance to the closest wind turbine.

Site	Date of colonies installation	Recording date	Apiary	Number of colonies	Distance to closest wind turbine (m)	Queen laying rate (%)
Le Pouzin	14.05.20	25.06.20	2	11	115	63.6
			4	12	140	75.0
			3	10	148	80.0
			5	14	239	78.6
			1	12	473	91.7
Bollène	18.05.20	24.06.20	2	14	114	100.0
			4	14	121	92.9
			1	14	153	85.7
			3	14	367	92.9
			5	14	409	64.3

Table 2. Average score for bee defensive behavior (gentleness and calmness on the comb) per apiary and site.

Apiary	Le Pouzin (02/06/2020)		Bollène (10/06/2020)	
	Gentleness	Calmness on the comb	Gentleness	Calmness on the comb
1	3.8	4	3.9	4
2	3.6	3.6	3.9	3.9
3	3.8	3.7	3.9	3.9
4	4	3.8	3.9	3.9
5	3.6	3.6	4	4

For the experiment carried out in Bollène, a total of 257 foragers tagged with a metallic chip were released. Two hours after the release of the foragers, the overall homing success was at 85.27% (n = 129 bee released) for the control group and at 67.97% (n = 128 bees released) for the treatment group.

The results of the GLMM show a significant negative effect of the distance from the hive on the rate of returning bees. For all groups of bees (control and exposed to wind turbines) taken together, the homing chance decreased as the release distance from the hive to which the bee belonged increased (Table 3). Passing by one, two or three turbines did not induce a negative effect on the homing rate of foragers itself as much as the wind speed, the temperature at the time released or the interaction of the factors of distance, temperature and wind speed, with the number of turbine footprints intersected.

Table 3. Generalized linear mixed models (GLMM) results conducted to assess the effects of wind turbines, release distance, temperature and wind speed at the time of bee release as well as their interactions on the homing success of bees at Le Pouzin **(A)** and Bollène **(B)** sites. The relative importance (RI) measures the occurrence frequency of each variable within the best candidate models (n = 26 for site A and n = 15 for site B), weighted by the respective statistical support of the model. A relative importance of 100% indicates that the variable appears in each of the best models and therefore receives maximal support as a potential explanatory factor in the homing failure.

	Parameters	Multimodel averaged estimate ± e.s.	*Z*	*P*	RI
Le Pouzin	Intercept	1.468 ± 0.574	2.549	**0.011**	–
	Turbine(s) intersected (Ti)	-0.164 ± 1.097	0.149	0.882	41.6%
	Release dist. (R)	-1.129 ± 0.971	1.159	0.246	50.4%
	Temperature (T)	0.726 ± 1.053	0.688	0.491	37.1%
	Wind speed (W)	-0.032 ± 0.777	0.041	0.968	28.9%
	Ti × R	3.075 ± 2.478	1.237	0.216	14.0%
	Ti × T	-3.262 ± 3.203	1.016	0.310	6.0%
	Ti × W	-6.423 ± 5.551	1.153	0.249	4.7%
Bollène	Intercept	3.707 ± 0.983	3.755	**<0.001**	–
	Turbine(s) intersected (Ti)	-4.717 ± 3.251	1.448	0.148	100%
	Release dist. (R)	-3.355 ± 0.902	3.702	**<0.001**	100%
	Temperature (T)	-0.557 ± 1.574	0.352	0.725	44.9%
	Wind speed (W)	-0.358 ± 1.247	0.286	0.775	51.4%
	Ti × R	1.647 ± 2.515	0.652	0.514	29.8%
	Ti × T	3.515 ± 2.129	1.644	0.100	25.0%
	Ti × W	7.234 ± 4.107	1.753	0.080	35.2%

4 Discussion

We assessed the effect of wind turbines on honey bees using important functions for the development of honey bee colonies including mating success using the egg-laying activity of young queens, weight gain of the colonies, bee behavior or the homing ability of foragers.

For the first experiment, the rate of laying queens at the end of the experiment was high and within the order of magnitude expected with 87.14% in Bollène and 77.97% in Le Pouzin. In comparison, Pérez-Sato & Ratnieks (2006) obtained a rate of 65% for laying queens (n = 40 colonies) on average 13 days after the introduction of virgin, maximum one day-old queens into the mating hives. Moreover, the laying activity of young queens did not differ between apiaries located at varying distances from the closest wind turbine, between 115 and 473 m in Le Pouzin and between 114 and 409 m in Bollène. An absence of laying activity of the queen can result from a fertility problem, from a mating failure or from her death. The wind turbines could have led to an absence or a reduction in queen laying activity by means of a direct lethal effect on the breeding bees during mating, by colliding with the turbines, or under the effect of turbulence. Such an impact on the survival of flying insects have been documented (Voigt 2021). This risk was identified for migrating insects or those with a high-altitude flight behavior at heights between 100 and 1200 m (Chapman et al. 2002). Such effects are less likely in this study. For the honey bee, mating occurs in congregations of males located at heights that vary between 4 and 40 m in altitude depending on the subspecies of the bee, the air temperature and the wind speed (Koeniger & Koeniger 2000). In this study, the turbine tower measures 80 m high and the blades are situated at a minimum of 35 m above the ground (blade length = 45 m). A risk of mortality with operating turbines could exist if congregations of males located near the turbines flew at the highest altitude. But as a whole, the bees succeeded in mating considering that there were no significant differences between apiaries in the rate of laying queens. The males from the outer apiaries (apiaries 1 and 5) and the queens from all of our experimental apiaries could reach each other to mate and the queens were able to return to their hives after mating.

This study was not intended to analyze the influence of wind turbines on foraging processes (recognition of flowers, recruitment of nestmates, resources collection …) that would need other studies. For example, the noise and vibrations produced by wind turbines could interfere with the sound signals emitted by the foragers during dances to recruit nestmates towards food sources (Kirchner 1993). However, our experiment colonies gained weight normally, regardless of their position and distance from the wind turbines. Weight gain means that resources were available and that colonies were healthy enough to establish food reserves (Quigley et al. 2019). Then, our results suggest that colonies placed near wind turbines are able to exploit the available food resources in the environment.

The bee behavior within the hive was also not altered and was comparable between apiaries. The observations and notes of the beekeepers confirmed the gentle and calm character of the bees at the two sites, 2 to 3 weeks after colonies were installed.

For the second experiment, the majority of foragers successfully returned to the hive two hours after their release. For all sites, the total homing rate was normal and varied between 68 and 85% for both the exposed and control bees. Our homing results can be compared to previous studies. For instance, homing performances varied from about 65 to 100% for foragers released 1 km-away from the hive (Pahl et al. 2011). Upon releasing the foragers at 500 m, Matsumoto (2013) recorded homing performances in control bees that varied between 60 to 90%. The statistical analyses did not show an impact of wind turbines on the homing flight of foragers. The wind turbines did not induce an increased disappearance of bees due to homing failure. The bees were released in such a way that the direct path towards the colony intersected the footprint of the turbines, due to the fact that the foragers would prefer the shortest path for returning to the hive by taking the straightest, most direct flight (Menzel et al. 2005). Without the constraint of wind, honey bees fly at an average speed of 6.8 m/s (von Frisch 1967) and at a low altitude of about 2 m above the ground (Garbuzov & Ratnieks 2014); this flying height decreases as the facing wind speed increases (Baird et al. 2021). The risk of direct impact by collision with the blades is therefore unlikely. Flower recognition, on the other hand, is partly based on the perception of odors (Chittka & Raine 2006) that could be disturbed by air movements near the blades.

In flight a forager uses sensory and cognitive abilities to navigate to a food source and to return successfully to the hive (von Frisch 1967). The navigation of a forager in flight first depends on its ability to learn the position of the hive in its environment according to the position of the sun and visual landscape features (Menzel 1993). The bee must then recall this initially-acquired information during the next, exploratory phase of orientation to find its way back. In this study, the wind turbines did not have an impact on the cognitive and spatial orientation abilities of the foragers returning to the hive (Capaldi & Dyer 1999). In particular our results do not support a change in homing behavior due to the flicker or strobe-like effects of the blade movement under sunny conditions or even due to the influence of electromagnetic fields produced. Electromagnetic fields of very low frequency found near powerlines ranging from 20 Microtesla (μT) to 100 μT (200 Milligauss (mG) to 1000 mG) have already been shown to affect olfactory learning abilities, flight, foraging activities and honey bee feeding (Shepherd et al. 2018). Close to the wind turbines, the level of measured electromagnetic fields range from 0.133 to 0.225 mG

(Knopper et al. 2014) and up to 1.1 mG (McCallum et al. 2014), which is much weaker than those recorded from powerlines, and could explain the lack of effect.

The release distance of foragers on the other hand was a factor influencing the homing results for the Bollène site. The homing success decreased as the distance increased for both exposed and control bees. It is indeed more complicated for the forager to orient and return to the hive as the release site moves further from the colony, even more so if the bee does not already know the way back (Pahl et al. 2011). In this study, we did not know if the foragers had a previous knowledge of the release point and the way back to the colony (bees familiar or not with the release sites). Indeed, each colony has its own foraging radius and thus a specific knowledge of the hive environment. Therefore it is possible that certain foragers had been released in an unfamiliar location which could explain the distance effect measured at the Bollène site, for which we recorded an abnormally low homing rate for two apiaries: 39% for the foragers from colony 1 released at 1699 m and 33.3% and 6.7% for bees released at distances of 523 and 924 m, respectively, from colony 3 (Table S2). The location of colony 3 at the most wind-exposed site could have equally participated in the low homing rates. For this colony, the low homing success rates recorded for exposed bees didn't influence the statistical results when excluded from the dataset.

To our knowledge, no published study has been conducted up until this point looking for the potential effects of wind turbines on the honey bee. Under the conditions of this study, wind turbines did not show any negative effects on the mating success, (queen egg-laying activity) development of the colonies (weight gain), bee behavior, nor homing success of foragers. The hypotheses of an increased mortality for foragers returning to the hive or for breeding bees when mating via collision with the turbines or due to the effect of turbulence generated by the blades would be unlikely here. Lastly, the results would suggest that the sounds, the electromagnetic fields or even the flicker or strobe-like effects from the blades movement would not lead to an impact on colony development. These results follow those from Pustkowiak et al. (2018) showing no effects of wind farms on abundance and diversity of pollinators communities. The results of this initial study are reassuring for the possibility of beekeepers positioning their hives in proximity to wind turbines. Additional studies would be necessary to confirm our results on wind farms with larger surface areas, higher densities of wind turbines and with different landscapes.

Acknowledgments: We thank C. Beri, C. Ferrus, P-A. Rault and C. Vidau for their help in the homing experiments, A. Sudan for providing the honey bee colonies, M. Pelissier for his technical help, C. Brun and M. Henry for their help with the corrections on the manuscript. We are grateful to C. McDonnell for her help with the English editing as well as the associate editor and three anonymous reviewers for comments and improvements on the manuscript. This research work was financially supported by the Compagnie Nationale du Rhône (CNR).

References

Baird, E., Boeddeker, N., & Srinivasan, M. V. (2021). The effect of optic flow cues on honeybee flight control in wind. *Proceedings of the Royal Society B: Biological Sciences, 288*(1943), 20203051. https://doi.org/10.1098/rspb.2020.3051

Barton, K. (2022). Multi-Model Inference. *Package "MuMIn"*, version 1.47.1

Bates, D., Mächler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., … Krivitsky, P. N. (2022). *lme4: linear mixed-effects models using "Eigen" and S4*. R package version 1.1-30.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach* (2nd ed.). New York: Springer.

Capaldi, E. A., & Dyer, F. C. (1999). The role of orientation flights on homing performance in honeybees. *The Journal of Experimental Biology, 202*(12), 1655–1666. https://doi.org/10.1242/jeb.202.12.1655

Chapman, J. W., Smith, A. D., Woiwod, I. P., Reynolds, D. R., & Riley, J. R. (2002). Development of vertical-looking radar technology for monitoring insect migration. *Computers and Electronics in Agriculture, 35*(2-3), 95–110. https://doi.org/10.1016/S0168-1699(02)00013-3

Chittka, L., & Raine, N. E. (2006). Recognition of flowers by pollinators. *Current Opinion in Plant Biology, 9*(4), 428–435. https://doi.org/10.1016/j.pbi.2006.05.002

Costa, C., Büchler, R., Berg, S., Bienkowska, M., Bouga, M., Bubalo, D., … Wilde, J. (2012). A europe-wide experiment for assessing the impact of genotype-environment interactions on the vitality and performance of honey bee colonies: Experimental design and trait evaluation. *Journal of Apicultural Science, 56*(1), 147–158. https://doi.org/10.2478/v10289-012-0015-9

European Commission (2011). Communication from the Commission to the European Parliament, The Council, The European Economic and Social Committee and the Committee of the regions. *Energy Roadmap 2050. COM(2011) 885 final*, Brussels.

European Commission, Directorate-General for Environment (2021). Guidance document on wind energy developments and EU nature legislation, Publications Office of the European Union. https://data.europa.eu/doi/10.2779/095188

Gallai, N., Salles, J.-M., Settele, J., & Vaissière, B. E. (2009). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics, 68*(3), 810–821. https://doi.org/10.1016/j.ecolecon.2008.06.014

Garbuzov, M., & Ratnieks, F. L. W. (2014). Lattice fence and hedge barriers around an apiary increase honey bee flight height and decrease stings to people nearby. *Journal of Apicultural Research, 53*(1), 67–74. https://doi.org/10.3896/IBRA.1.53.1.06

Guest, E. E., Stamps, B. F., Durish, N. D., Hale, A. M., Hein, C. D., Morton, B. P., … Fritts, S. R. (2022). An updated review of hypotheses regarding bat attraction to wind turbines. *Animals (Basel), 12*(3), 343. https://doi.org/10.3390/ani12030343

Henry, M., Bertrand, C., Le Féon, V., Requier, F., Odoux, J.-F., Aupinel, P., … Decourtye, A. (2014). Pesticide risk assessment in free-ranging bees is weather and landscape dependent. *Nature Communications, 5*(1), 4359. https://doi.org/10.1038/ncomms5359

Hunt, J. H., & Richard, F.-J. (2013). Intracolony vibroacoustic communication in social insects. *Insectes Sociaux, 60*(4), 403–417. https://doi.org/10.1007/s00040-013-0311-9

Kirchner, W. H. (1993). Acoustical communication in honeybees. *Apidologie, 24*(3), 297–307. Retrieved from https://hal.archives-ouvertes.fr/hal-00891076 https://doi.org/10.1051/apido:19930309

Kirchner, W. H., Dreller, C., & Towne, W. F. (1991). Hearing in honeybees: Operant conditioning and spontaneous reactions to airborne sound. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology, 168*(1), 85–89. https://doi.org/10.1007/BF00217106

Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings. Biological Sciences, 274*(1608), 303–313. https://doi.org/10.1098/rspb.2006.3721

Knopper, L. D., Ollson, C. A., McCallum, L. C., Whitfield Aslund, M. L., Berger, R. G., Souweine, K., & McDaniel, M. (2014). Wind turbines and human health. *Frontiers in Public Health, 2*, 63. https://doi.org/10.3389/fpubh.2014.00063

Koeniger, N., & Koeniger, G. (2000). Reproductive isolation among species of the genus Apis. *Apidologie, 31*(2), 313–339. https://doi.org/10.1051/apido:2000125

Leroux, C., Kerbiriou, C., Le Viol, I., Valet, N., & Barré, K. (2022). Distance to hedgerows drives local repulsion and attraction of wind turbines on bats: Implications for spatial siting. *Journal of Applied Ecology, 59*(8), 2142–2153. https://doi.org/10.1111/1365-2664.14227

Long, C. V., Flint, J. A., & Lepper, P. A. (2011). Insect attraction to wind turbines: Does colour play a role? *European Journal of Wildlife Research, 57*(2), 323–331. https://doi.org/10.1007/s10344-010-0432-7

Marques, A. T., Santos, C. D., Hanssen, F., Muñoz, A.-R., Onrubia, A., Wikelski, M., … Silva, J. P. (2020). Wind turbines cause functional habitat loss for migratory soaring birds. *Journal of Animal Ecology, 89*(1), 93–103. https://doi.org/10.1111/1365-2656.12961

Matsumoto, T. (2013). Reduction in homing flights in the honey bee *Apis mellifera* after a sublethal dose of neonicotinoid insecticides. *Bulletin of Insectology, 66*(1), 1–9.

McCallum, L. C., Whitfield Aslund, M. L., Knopper, L. D., Ferguson, G. M., & Ollson, C. A. (2014). Measuring electromagnetic fields (EMF) around wind turbines in Canada : Is there a human health concern? *Environmental Health, 13*(1), 9. https://doi.org/10.1186/1476-069X-13-9

Menzel, R. (1993). Associative learning in honey bees. *Apidologie, 24*(3), 157–168. https://doi.org/10.1051/apido:19930301

Menzel, R., Greggers, U., Smith, A., Berger, S., Brandt, R., Brunke, S., … Watzl, S. (2005). Honey bees navigate according to a map-like spatial memory. *Proceedings of the National Academy of Sciences of the United States of America, 102*(8), 3040–3045. https://doi.org/10.1073/pnas.0408550102

OECD (2021). Guidance document on honey bee (Apis mellifera L.) homing flight test, using single oral exposure to sublethal doses of test chemical. *OECD Publishing Series on Testing and Assessment, 332*.

OEPP/EPPO (2010). Side-effects on honeybees. *Bulletin OEPP. EPPO Bulletin. European and Mediterranean Plant Protection Organisation, 40*(3), 313–319. Retrieved from https://pp1.eppo.int/standards/PP1-170-4-en.pdf https://doi.org/10.1111/j.1365-2338.2010.02418.x

Osborne, J. L. (2012). Bumblebees and pesticides. *Nature, 491*(7422), 43–45. https://doi.org/10.1038/nature11637

Pahl, M., Zhu, H., Tautz, J., & Zhang, S. (2011). Large scale homing in honeybees. *PLoS One, 6*(5), e19669. https://doi.org/10.1371/journal.pone.0019669

Pérez-Sato, J. A., & Ratnieks, F. L. W. (2006). Comparing alternative methods of introducing virgin queens (Apis mellifera) into mating nucleus hives. *Apidologie, 37*(5), 571–576. https://doi.org/10.1051/apido:2006036

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution, 25*(6), 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Pustkowiak, S., Banaszak-Cibicka, W., Mielczarek, Ł. E., Tryjanowski, P., & Skórka, P. (2018). The association of windmills with conservation of pollinating insects and wild plants in homogeneous farmland of western Poland. *Environmental Science and Pollution Research International, 25*(7), 6273–6284. https://doi.org/10.1007/s11356-017-0864-7

Quigley, T. P., Amdam, G. V., & Harwood, G. H. (2019). Honey bees as bioindicators of changing global agricultural landscapes. *Current Opinion in Insect Science, 35*, 132–137. https://doi.org/10.1016/j.cois.2019.08.012

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rollin, O., Bretagnolle, V., Decourtye, A., Aptel, J., Michel, N., Vaissière, B. E., & Henry, M. (2013). Differences of floral resource use between honey bees and wild bees in an intensive farming system. *Agriculture, Ecosystems & Environment, 179*, 78–86. https://doi.org/10.1016/j.agee.2013.07.007

Schmidt, J. H., & Klokker, M. (2014). Health effects related to wind turbine noise exposure: A systematic review. *PLoS One, 9*(12), e114183. https://doi.org/10.1371/journal.pone.0114183

Schuster, E., Bulling, L., & Köppel, J. (2015). Consolidating the state of knowledge: A synoptical review of wind energy's wildlife effects. *Environmental Management, 56*(2), 300–331. https://doi.org/10.1007/s00267-015-0501-5

Shepherd, S., Lima, M. A. P., Oliveira, E. E., Sharkh, S. M., Jackson, C. W., & Newland, P. L. (2018). Extremely low frequency electromagnetic fields impair the cognitive and motor abilities of honey bees. *Scientific Reports, 8*(1), 7932. https://doi.org/10.1038/s41598-018-26185-y

Tan, K., Yang, S., Wang, Z.-W., Radloff, S. E., & Oldroyd, B. P. (2012). Differences in foraging and broodnest temperature in the honey bees Apis cerana and A. mellifera. *Apidologie, 43*(6), 618–623. https://doi.org/10.1007/s13592-012-0136-y

Voigt, C. C. (2021). Insect fatalities at wind turbines as biodiversity sinks. *Conservation Science and Practice, 3*(5), e366. https://doi.org/10.1111/csp2.366

von Frisch, K. (1967). *The dance language and orientation of bees*. Cambridge, MA: Harvard University Press.

WindEurope (2022). *Wind energy in Europe, 2021 statistics and the outlook for 2022–2026*. https://windeurope.org/intelligence-platform/reports/

Zwart, M. C., Dunn, J. C., McGowan, P. J. K., & Whittingham, M. J. (2016). Wind farm noise suppresses territorial defense behavior in a songbird. *Behavioral Ecology, 27*(1), 101–108. https://doi.org/10.1093/beheco/arv128

Manuscript received: 8 October 2022
Revisions requested: 27 November 2022
Modified version received: 14 April 2023
Accepted: 2 August 2023

The pdf version (Adobe JavaScript must be enabled) of this paper includes an electronic supplement:
Table S1–S4