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RESEARCH ARTICLE

Insectivorous bats alter their flight and feeding behaviour at ground-mounted solar farms

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Abstract

1. Efforts to mitigate the climate crisis result in a green-green dilemma: the development of renewable energy technology is required worldwide to reduce greenhouse gas emissions but can have negative impacts on biodiversity. Impacts are being documented for wind farms, but effects of solar farms (photovoltaic power stations) on habitat use of vertebrates remain extremely poorly known.
2. Using insectivorous bats as a biological model for high trophic levels, we tested whether the presence of ground-mounted solar farms affected flight and feeding behaviour. We assessed behaviour using three-dimensional flight path reconstruction systems from echolocation calls, via standardised paired sampling of 16 control and 16 solar farm (treatment) sites. We quantified bat flight and feeding behaviour as flight speed, sinuosity of flight trajectories, and the probability of emission of feeding buzzes (acoustic signatures of prey capture attempts), and demonstrated that feeding was characterised by slow, sinuous flight with feeding buzzes.
3. We recorded 15,273 three-dimensional bat positions, resulting in 1317 flight trajectories. We found strong behavioural responses to ground-mounted solar farms in two of three bat guilds and five of seven taxa. Specifically, bats shifted their flight towards faster (+10 to +44%) and straighter trajectories (+33%) with lower probability of prey capture attempts (−18 to −39%) at solar farms.
4. Since these changes in flight features are explicit indicators of a decrease in bat feeding behaviour, the implementation of ground-mounted solar farms is likely to result in reduced feeding habitat quality for bats.
5. *Synthesis and applications:* The negative effects of solar farms on bat flight and feeding behaviour should be considered when solar energy projects are planned. Research is needed to understand the mechanisms underlying the effects; for example, shading underneath solar panels may reduce plant biomass and therefore insect prey availability. Until exact mechanisms are identified, efforts should be made, first to avoid building solar farms on sites with great feeding potential

Kévin Barré and Alice Baudouin share joint first authorship on this work.

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for bats, and second to offset residual effects by improving the surrounding land and/or solar farms to provide better foraging opportunities. In this way, populations of bats can be supported alongside the generation of renewable energy.

KEYWORDS

Chiroptera, feeding buzz, foraging behaviour, functionality loss, green-green dilemma, movement, renewable solar energy, three-dimensional (3D) acoustic tracking

1 | INTRODUCTION

The current climate crisis is driving the exponential development of renewable energy technologies worldwide, aimed at reducing our reliance on fossil energy and drastically reducing greenhouse gas emissions (IPCC, 2022). In the European Union, new policy initiatives have been implemented through the European Green Pact, with an ambitious aim of climate neutrality by 2050, which should result in a 40% increase in the share of renewable energy by 2030. In response to the current geopolitical context and the increasing need for energy independence, this pact has been further strengthened by the REPowerEU plan, which elevates the target to 45%. Although using renewable energy sources (i.e. solar, wind, geothermal, hydro, ocean and biomass) can contribute to the reduction in greenhouse gas emissions, the technology required is not exempt from negative impacts on biodiversity, thus generating a green-green dilemma (Gibson et al., 2017). This dilemma is particularly complex as the climate crisis is also accompanied by a biodiversity crisis; it is now recognised that these crises are interconnected and should be addressed together (Pörtner et al., 2021).

The impact of wind farms on biodiversity, and especially on flying fauna, is well-evidenced (Katzner et al., 2019; Voigt & Kingston, 2015), but responses of biodiversity to solar farms (photovoltaic power stations) remain poorly documented. There is an urgent need to understand how ground-mounted solar farms affect biodiversity, as the exponential growth of this renewable energy source is resulting in large-scale land-use conversion throughout Europe and elsewhere (IRENA, 2020). Ground-mounted solar farms could affect biodiversity in several ways, either directly due to the structures themselves or indirectly through changes induced by the structures. For instance, indirect effects could result from shade produced by solar panels inducing a shift in plant communities (Uldrijan et al., 2021) and a reduction in plant biomass and blooming (Armstrong et al., 2016; Graham et al., 2021). Solar panels can also attract diurnal aquatic insects through the polarised light they generate; thus, they represent an ecological trap (Horváth et al., 2010). Pollinator abundance, richness and diversity are strongly reduced underneath solar panel rows (i.e. in full shade conditions), and soil disturbance and vegetation removal during solar farm development displaces insect flower visitors (Graham et al., 2021; Grodsky et al., 2021). Finally, solar farms can create sensory traps for flying vertebrates (birds and bats) leading to attempts to drink from the smooth, horizontal panels or collisions with smooth, vertical panels

(Greif et al., 2017), potentially generating additional energy costs. Collisions with panels also pose fatality risks (Smallwood, 2022).

Despite the important synthesis and review work of Smallwood (2022), effects of the installation of solar farms on habitat use by vertebrates remain poorly documented. There have been only three studies: one shows that solar farms lead to reduced bird species richness and density (Visser et al., 2019), and two show that they lead to reduced activity of several insectivorous bat species (Szabadi et al., 2023; Tinsley et al., 2023). Perturbations of insectivorous bats, which occupy high trophic levels, are likely to be linked to reductions in the abundance of their insect prey, which could be generated by reduced plant biomass in the shady conditions under solar panels (Armstrong et al., 2016; Graham et al., 2021). Bats represent a biological model that is very sensitive to local changes in prey distribution and have the ability to select suitable patches for foraging at a fine scale (Barré et al., 2017). Following this hypothesis, insectivorous bats at solar farms should exhibit less foraging behaviour than those in the surrounding semi-natural habitats without solar panels. An explicit way to study bat foraging behaviour is to quantify the acoustic signatures of bats' prey capture attempts (hereafter referred to as 'feeding buzzes') in recordings of their echolocation calls. Tools have recently been developed to detect feeding buzzes automatically from the characteristics of the calls (Roemer et al., 2021), but feeding buzzes can be rare (they usually make up <2% of acoustic recordings; Barré et al., 2020). Other behavioural metrics increasingly used in bat research, such as flight speed and sinuosity (Barré et al., 2020; Gilmour et al., 2021; Grodzinski et al., 2009; Polak et al., 2011), may be effective proxies of feeding flight, as has been demonstrated for *Pipistrellus kuhlii* and *Myotis daubentonii* (Grodzinski et al., 2009; Jones & Rayner, 1988). More specifically, feeding flight is expected to be associated with lower flight speed and higher flight sinuosity than commuting flight. Since such changes in flight behaviour could also mirror obstacle avoidance (Falk et al., 2014), flight speed and sinuosity in bats can be considered as complementary metrics to feeding buzzes in the detection and quantification of feeding behaviour.

We aimed to assess the effects of ground-mounted utility-scale solar farms on bat feeding behaviour by using three-dimensional flight path reconstruction systems from echolocation calls, through a paired sampling design. We quantified bat feeding behaviour by using the probability of feeding buzz emission, flight speed and sinuosity of flight trajectories. To check the validity of these three metrics as indicators of feeding behaviour in our data, we first assessed

the extent to which flight speed and sinuosity were related to the probability of feeding buzz emission. We hypothesised that decreasing flight speed and increasing flight sinuosity would be associated with an increasing probability of detecting feeding buzzes. Then, we predicted that feeding buzz emission and flight trajectory sinuosity would be lower, and flight speed would be higher, at solar farms than at control sites, as the insect prey resource was expected to be less abundant at sites in which less light reached the ground due to shading by solar panels.

2 | MATERIALS AND METHODS

2.1 | Study area

With permission from the Compagnie Nationale du Rhône (CNR, a solar farm management company), the study was carried out at nine ground-mounted utility-scale solar farms in the Rhône Valley in France (Figure 1a,b), a region supporting high activity of several bat species, including *P. kuhlii*, *Pipistrellus nathusii* and *Pipistrellus pygmaeus* (Bas et al., 2022). We selected solar farms for which treatment and control sites could be standardised regarding landscape composition and distance to foraging habitats (e.g. water bodies and woodland edges) so that similar sites could be found to form each pair (see Section 2.2 for more details). We have ensured that there are no obstacles to bat flight other than the solar panels in control and treatment sites. The surface areas of the solar farms varied between 2.5 and 25 ha (median=7.4 ha); their capacities varied between 2.5 MW and 14 MW (median=4.2 MW). Seven of the nine solar farms had fixed-angle panels (roughly 25°), the other two had mobile-angle (mono-axial) panels on the east-west axis (placed horizontally during surveys). The surface of the panels was rough, with fine crenulations. Solar panels were on average 2.4 ± 0.4 m high (mean \pm standard deviation) and 3.4 ± 1.1 m wide; the distance between the solar panel rows was 4.9 ± 1.3 m. Solar panels were installed on grazed or mown grasslands sown with native plant species which were 0.2 to 1.1 m in height and covered 20 to 90% of the ground surface (Table S1). The sites used for solar farms were either old industrial sites or embankments resulting from the canalisation of the River Rhône and were located 233 ± 192 m from the river bank. At the landscape scale (500 m around the study sites), the land use was dominated by agricultural land (44%), woodland (34%) and impervious surfaces (16%).

2.2 | Sampling design and three-dimensional acoustic tracking

To assess the effects of ground-mounted solar farms on bat feeding behaviour, we implemented a paired sampling design, each pair consisting of one site within a solar farm (treatment) and one matched control site located outside the farm (control; Figure 1c). Solar and control sites within a pair were separated by at least 100 m

(to avoid simultaneous double counting of bats) and by no more than 500 m and were sampled simultaneously on the same night, in order to avoid differences in weather conditions and landscape context between solar and control sites. For each pair, we standardised the vegetation height and cover at the sampling location using visual estimations made by two observers (Alice Baudouin and Kévin Barré), the distance to the nearest woodland edge and water body and the proportion of woodland (both coniferous and deciduous) within a 1000 m radius. These parameters were statistically similar in the two sites of each pair (Table S1). Each night, we sampled one or two pairs simultaneously, at one solar farm, during the first 3 h after sunset. In total, 16 pairs (16 control and 16 solar sites) were sampled on nine nights from September 21st to 30th, 2022, during suitable weather conditions for insects and bats (mean temperature at night: 11.4–20°C; wind speed: 0–5.5 m/s; no rain; Table S1).

We acoustically monitored bat flight trajectories by recording three-dimensional positions of bats using the Trajecto V1 system (hereafter called 'the microphone array') from Suva-tech (Phnom-Penh, Cambodia; <https://www.suva-tech.com/>). This built-in system contains four microphones (FG 23329, Knowles Acoustics, Itasca, IL USA), which record bat echolocation calls from 1 to 250 kHz. The microphones in the array were arranged in a horizontal triangle shape, with one microphone in each corner and one in the middle (Figure 1d). At solar sites, the microphone array was always placed in the middle of a gap between two rows of solar panels, at more than 25 m from the edge of the solar farm, with the x axis (Figure 1d) oriented parallel to the rows of panels. We used the same placement pattern in term of microphone arrangement and x axis azimuth at control sites. Within the detection range (roughly 30 m radius), bat positions were continuously assessed by the system using the time difference of arrival of bat echolocation calls between microphones (Ing et al., 2016; Koblitz, 2018). From three-dimensional positions, we reconstructed complete bat flight trajectories following the approach described by Barré et al. (2020, 2021). In total during the study, flight trajectories were 3.2 ± 2.9 s in duration and contained 11.6 ± 8.3 positions (i.e. echolocation calls). Solar panels can prevent sound propagation, creating 'acoustic blind spots' in which echolocation calls cannot be detected if a panel is present between the bat and the microphone. Hence, on solar sites, the sphere of acoustic detection was truncated by acoustic blind spots. In order to avoid differences in detection volumes between control and solar sites, we filtered out the three-dimensional positions at each control site where bats could not be detected at its paired solar site because of the acoustic blind spots. Specifically, locations of bats at a control site that corresponded to a location behind a panel at the paired solar site were eliminated.

2.3 | Assigning species and feeding buzz probability to trajectories

Each bat recording made via the microphone array, in the form of a half-second sound file, was classified to the closest taxonomic level using

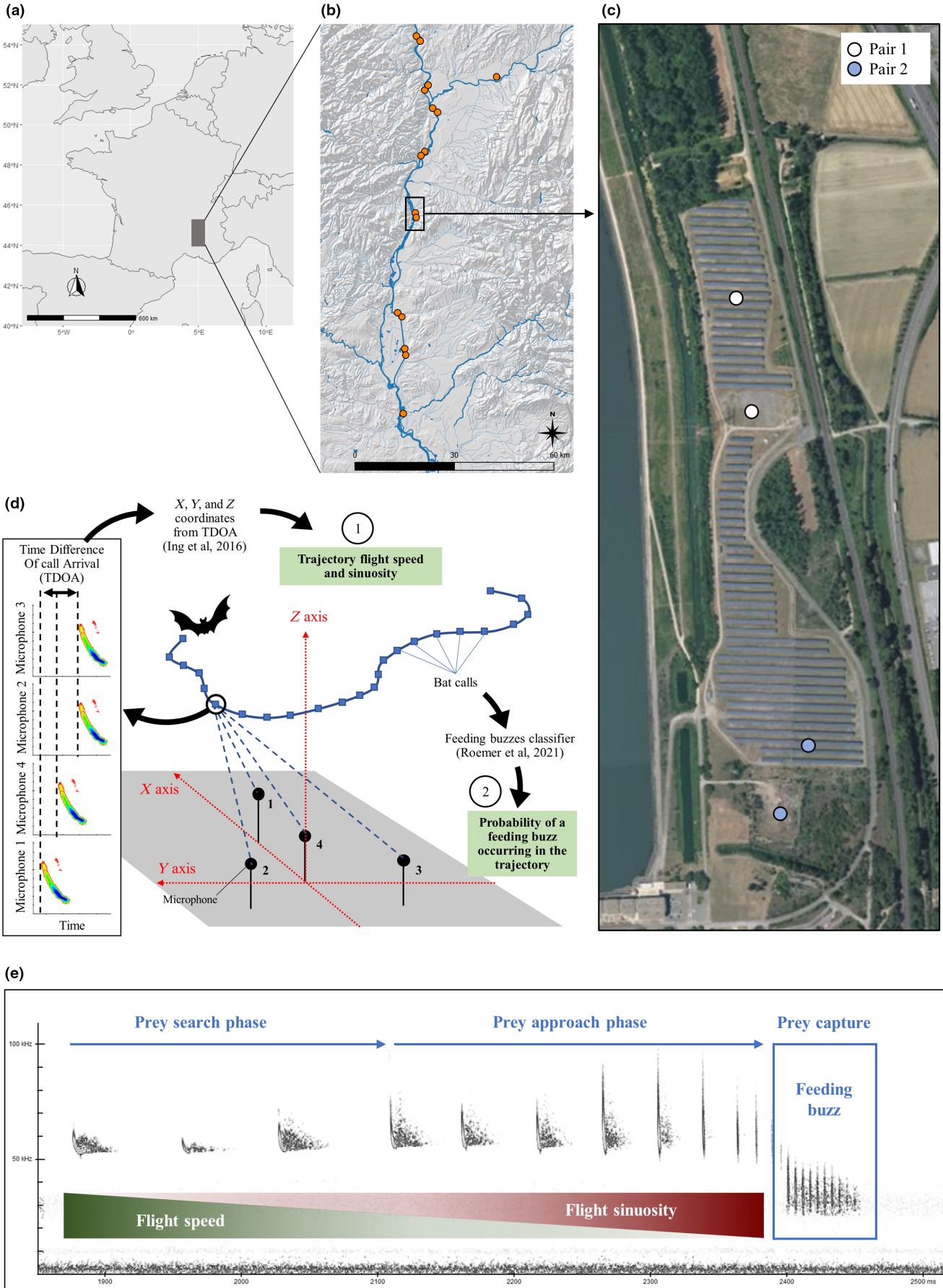


FIGURE 1 Map of the study area (a) and the 16 pairs of solar farms sampled for bats by using the microphone arrays (b), an example of two pairs sampled the same night (c), a schematic overview of the set-up used to reconstruct bat trajectories and compute behavioural metrics from echolocation calls (d), and a spectrogram showing the expected change in flight behaviour within a trajectory from prey search phase echolocation calls to the feeding buzz emission phase for prey capture: as flight speed decreases during the search and approach phase before a feeding buzz, sinuosity increases (e).

the Tadarida software (Bas et al., 2017), and assigned a feeding buzz probability using a sonotype classifier (Roemer et al., 2021). The probability of feeding buzz emission was calculated by the classifier based on the prey capture phase (i.e. the feeding buzz itself) following the prey approach phase, which is characterised by deceleration (Figure 1e; Jones & Rayner, 1988). Then, we linked each identification and buzz probability to a trajectory based on the same sound file. When several bat identifications were proposed for a single trajectory, we associated each trajectory with the single species that was most represented and had the highest automated identification confidence score.

Identification of bats to the species level from echolocation calls is problematic for some species, so we limited the identification level of species belonging to the *Myotis* genus to *Myotis* spp. To increase the generality of the results and the value of the data, we also pooled species into three functional guilds based on their echolocation call structure and foraging strategies: long-range echolocators (LRE, including open-space species from *Eptesicus* and *Nyctalus* genus), mid-range echolocators (MRE, including edge-space species from the *Pipistrellus* genus, *Hypsugo savii* and *Miniopterus schreibersii*), and short-range echolocators (SRE, including narrow-space species from *Myotis* and *Plecotus* genus and *Barbastellus barbastella*). We restricted the analyses to six species (*Pipistrellus pipistrellus*, *Pipistrellus kuhlii*, *Pipistrellus nathusii*, *Pipistrellus pygmaeus*, *Nyctalus leisleri* and *Plecotus austriacus*), one species group (*Myotis* spp.) and three guilds (LRE, MRE and SRE), for which the number of trajectories recorded was higher than the number of sites (Table S2).

2.4 | Computing flight behaviour metrics

Based on the three-dimensional positions of bats in reconstructed trajectories, we computed (i) mean trajectory flight speed, (ii) minimum trajectory flight speed and (iii) trajectory sinuosity. Flight speed (V) between two positions was computed as follows (Equation 1):

$$V_i = \frac{\sqrt{(x_i - x_j)^2 + (y_i - y_j)^2 + (z_i - z_j)^2}}{t_i - t_j} \quad (1)$$

where x , y and z represent distances to microphone 1 (Figure 1d) for each of the three-dimensional axes, and t is the time of call arrival to the microphone array of a given position i and its previous position j .

The sinuosity of the trajectory (S) was computed as follows (Equation 2):

$$St = \frac{\sum_{i=2}^N \sqrt{(x_i - x_{i-1})^2 + (y_i - y_{i-1})^2 + (z_i - z_{i-1})^2}}{\sqrt{(x_N - x_1)^2 + (y_N - y_1)^2 + (z_N - z_1)^2}} \quad (2)$$

where x , y and z represent distances to microphone 1 for each of the three-dimensional axes, N is the last position of the trajectory t , while 1 is the first position and i is the number of each individual position starting from the second position.

When computing average flight speed of the bat in each trajectory, we filtered out positions with flight speed >20 m/s, as higher values are unlikely to be accurate (O'Mara et al., 2021); this resulted in us removing 25.5% of positions and 2% of trajectories. Similarly, we filtered out trajectories with sinuosity values higher than the 95% quantile of this metric (i.e. values of >70), to eliminate outliers.

Finally, based on automated classification of feeding buzz probability, we computed the (iv) mean feeding buzz probability and (v) maximum feeding buzz probability for each trajectory.

2.5 | Statistical analysis

To test for effects of the presence of photovoltaic panels on bat feeding behaviour, we conducted statistical analysis following three steps. First, we assessed the robustness of the feeding buzz probability produced by the automated classifier as an indicator of the real feeding behaviour. Second, we assessed the extent to which the other flight behaviour metrics (flight speed and trajectory sinuosity) were effective proxies of feeding behaviour. Finally, we tested whether the feeding buzz probability and flight behaviour metrics differed between solar and control sites. The following sections present these three analysis steps.

2.5.1 | Robustness of the feeding buzz probability estimation

We first assessed the extent to which feeding buzz probability produced by the classifier built by Roemer et al. (2021) was a good indicator of feeding behaviour. To do this, we modelled the relationship between 141 stratified manual checks of buzz presence/absence made by the authors and the buzz probability provided by the classifier, using generalised linear models associated with a binomial distribution (R package lme4).

2.5.2 | Relationships between feeding buzz probability and flight behaviour metrics

Since flight behaviour metrics (i.e. trajectory flight speed and sinuosity) have seldom been tested as proxies of feeding behaviour, we first modelled the relationships between the mean and maximum feeding buzz probability as response variables, and (i) mean trajectory flight

speed, (ii) minimum trajectory flight speed and (iii) trajectory sinuosity as explanatory variables, using Generalised Linear Mixed Models (GLMM; R package *glmmTMB*) associated with Gaussian distributions. We included the pair identifier as a random effect to account for the paired sampling design, and the quadratic terms of each explanatory variable, as we expected nonlinear relationships.

2.5.3 | Effects of solar farms on bat flight and feeding behaviour

We assessed whether bat feeding behaviour differed between solar and control sites. To do this, we built GLMMs using either mean or minimum trajectory flight speed, trajectory sinuosity, or mean or maximum feeding buzz probability as response variables, and the type of site (i.e. solar or control) as the explanatory variable. We used Gaussian distributions for mean and minimum flight speed and sinuosity, and beta distributions for mean and maximum feeding buzz probability. We included the pair identifier as a random effect, and, when required, we adapted the weight of response variables to the associated precision of positions (i.e. with the inverse of the imprecision squared, to give more weight to the most precise positions; Barré et al., 2020, 2021) by adding a precision weight term in GLMMs (see Supporting Information S1 for more details). For Gaussian models, we normalised response variables using the best transformation method, assessed using the R package *bestNormalize*. Finally, we checked that residuals of models did not exhibit issues using the R package *DHARMa*. All analyses were performed with R v.4.2.0 (R Core Team, 2020).

3 | RESULTS

3.1 | Three-dimensional acoustic tracking

We recorded a total of 15,273 bat positions. Of these, 87% were produced by mid-range echolocators (MRE): *P. nathusii* (38%) and *P. pygmaeus* (37%) were the most represented, followed by *P. kuhlii* (14%) and *P. pipistrellus* (11%). Short-range echolocators (SRE) produced 7% of positions, which were shared between *Myotis* spp. (57%) and *P. austriacus* (35%). Long-range echolocators (LRE) produced 5% of positions: *N. leisleri* was dominant (79%), followed by *N. noctula* (11%). From the three-dimensional positions we reconstructed a total of 1317 trajectories, mainly of MRE (82%), followed by SRE (9%) and LRE (9%) (Table S2). On average, trajectories contained 12.5 positions for MRE, nine positions for SRE, and six positions for LRE.

3.2 | Robustness of feeding buzz probability estimations and correlations with flight behaviour metrics

We found that the feeding buzz probability from the automated classifier reliably estimated the probability of feeding buzz presence

as assessed by manual checks, with a strong positive relationship (classifier probabilities of 0 and 1 corresponded to buzz detection success probabilities of 0.08 and 0.99, respectively; $p = 2.04 \times 10^{-8}$, estimate \pm SE = 3.96 ± 0.71 ; Figure 2a). Further analyses confirmed that the flight behaviour metrics flight speed and trajectory sinuosity were relevant predictors of feeding behaviour. Specifically, we found that increasing mean or maximum feeding buzz probability in the trajectory was correlated with decreasing trajectory flight speed (Figure 2b,c,e,f; Table S3) and increasing trajectory sinuosity (Figure 2d,g; Table S3). Therefore, feeding was characterised by slow, sinuous flight with feeding buzzes.

3.3 | Effect of solar farms on bat flight and feeding behaviour

For five bat taxa (*P. kuhlii*, *P. pygmaeus*, *P. austriacus*, and the guilds MRE and SRE), we found that mean flight speed was significantly higher at solar sites than at control sites. Mean flight speed was significantly lower at solar sites than at control sites for *P. nathusii* (Figure 3a; Table 1 and Table S4). Minimum flight speed was significantly higher at solar sites than at control sites for the SRE guild, *P. kuhlii*, *P. pygmaeus* and *P. austriacus* (Figure 3b; Table 1 and Table S4).

We also found that mean feeding buzz probability of the trajectory was significantly lower at solar sites than at control sites for the MRE guild, *P. nathusii* and *P. pipistrellus*, and the same pattern was found for the maximum feeding buzz probability of the trajectory for *P. pipistrellus* (Figure 3c,d; Table 1 and Table S4). Furthermore, the trajectory sinuosity was significantly lower at solar sites than at control sites for the SRE guild only (Figure 3e; Table 1 and Table S4).

4 | DISCUSSION

In line with our hypothesis, insectivorous bats of several species in two functional guilds showed strong behavioural responses to ground-mounted utility-scale solar farms, by shifting their flight towards faster and straighter trajectories with lower probability of feeding buzz emission. Since these changes in flight features are explicit indicators of a decrease in bat feeding behaviour, it is clear that the implementation of solar farms results in a reduction of habitat quality for bats.

A mechanism to explain the reduced feeding flight behaviour at solar farms could be the reduction of prey biomass by trophic cascade. This mechanism is consistent with studies showing a reduction of global biomass, floral abundance and blooms in plant communities underneath solar panels (Armstrong et al., 2016; Graham et al., 2021), which could, in turn, reduce insect prey availability (Graham et al., 2021). However, this mechanism must be interpreted with caution, as Graham et al. (2021) only studied diurnal pollinators, and no researchers, to our knowledge, have

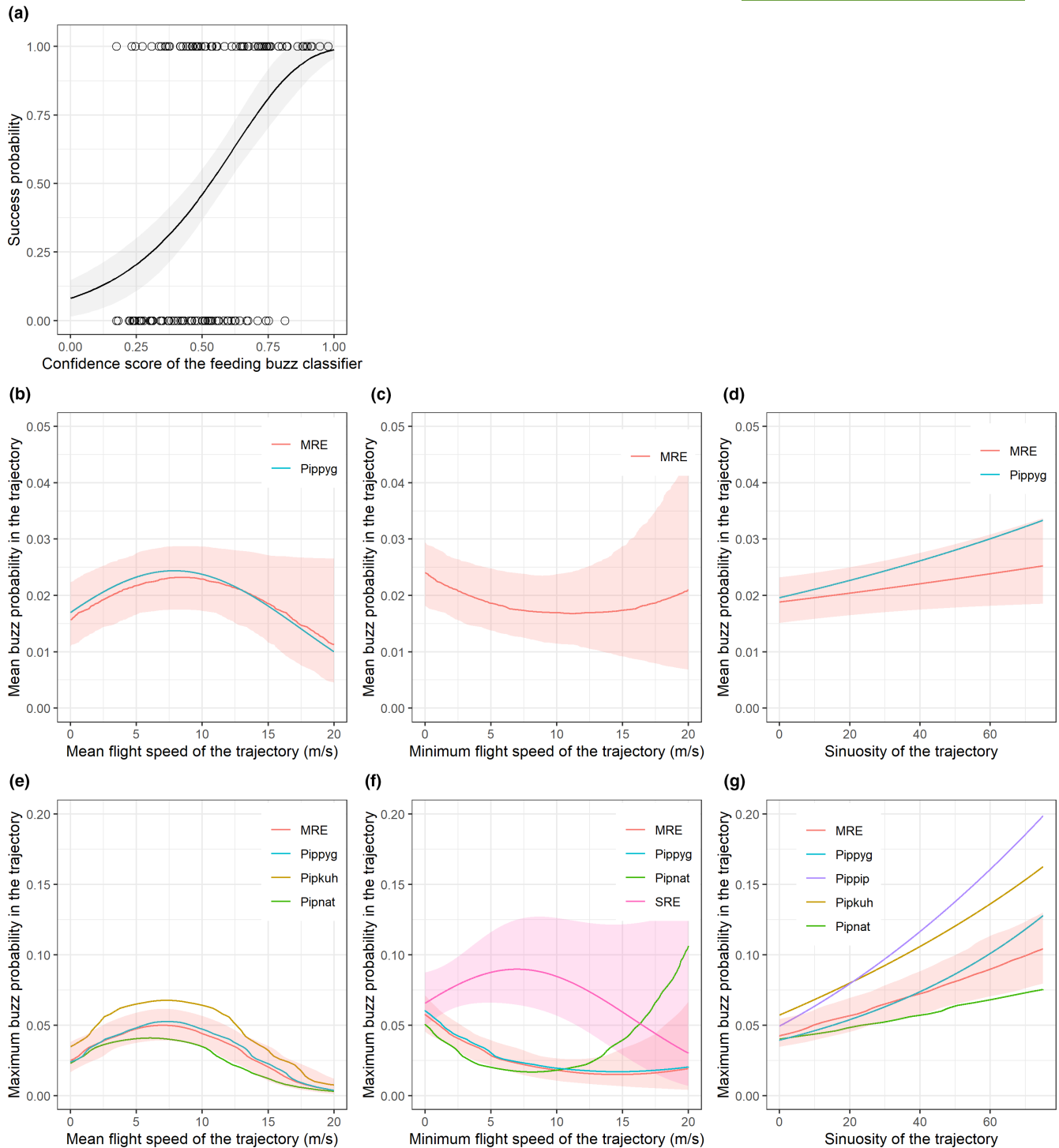


FIGURE 2 Feeding by bats is characterised by slow, sinuous flight with feeding buzzes. Test of the robustness of bat feeding buzz probability estimation, using logistic regression to compare success probability from manual checks with the confidence score of the feeding buzz classifier from automated identification (Roemer et al., 2021; a). Relationships between the mean (b–d) and maximum (e–g) feeding buzz probability of the trajectory, and the mean flight speed (b, e), the minimum flight speed (c, f), and the sinuosity of the trajectory (d, g), from generalised linear mixed models for bat guilds and species (MRE: mid-range echolocators; Pippyg: *P. pygmaeus*; Pippip: *P. pipistrellus*; Pipkuh: *P. kuhlii*; Pipnat: *P. nathusii*; SRE: short-range echolocators). Only significant effects ($p < 0.05$) are represented, and 95% confidence intervals are shown as shaded areas for guilds.

assessed variation in the abundance of the nocturnal insects that are potential prey for bats in response to solar farms. An alternative hypothesis is that insects are attracted by the polarised

light produced by the smooth surface of solar panels (Horváth et al., 2010). Such an attraction could reduce the amount of insects available in the aerial volume at solar farms by concentrating

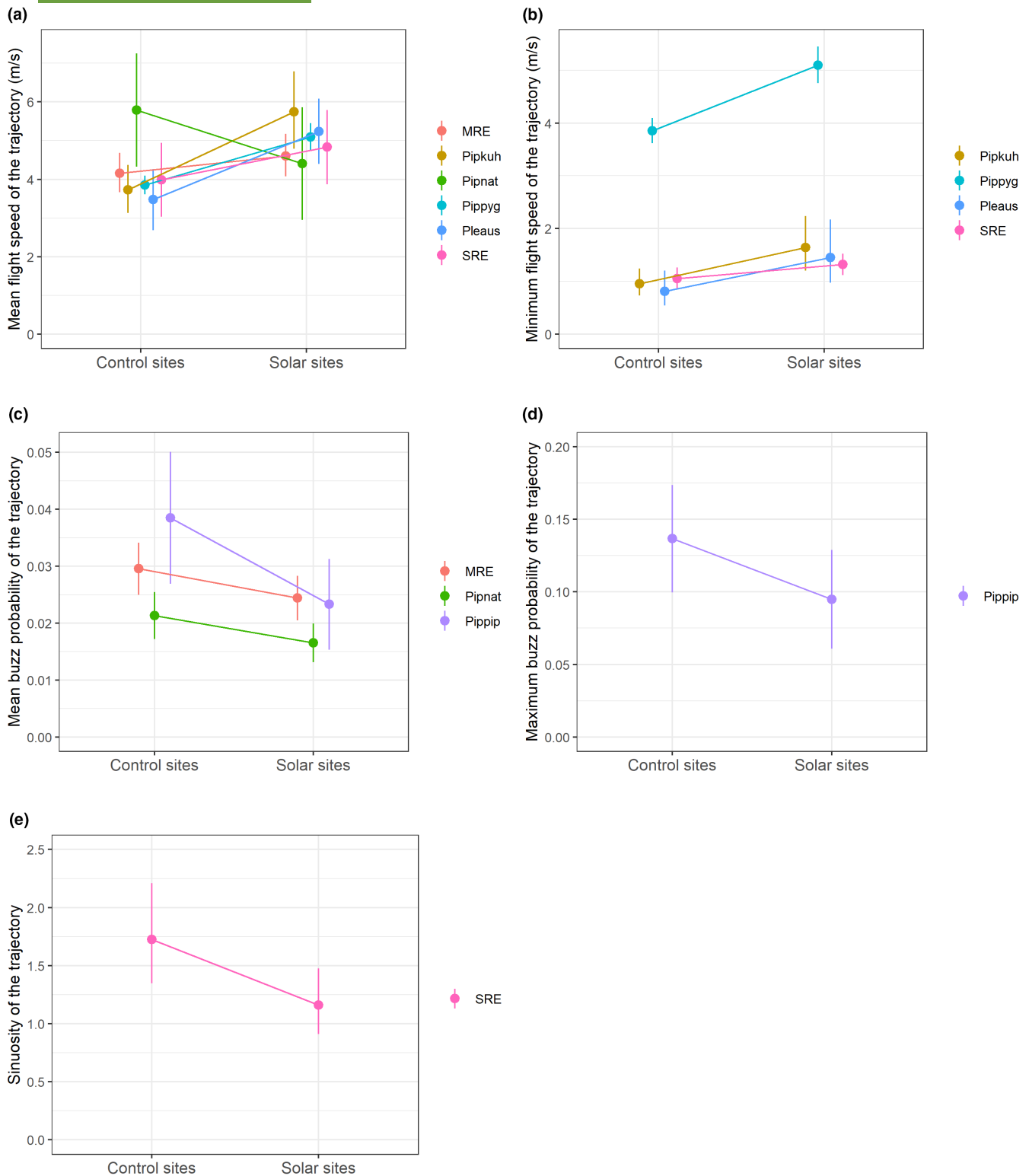


FIGURE 3 Effects of solar farms on the flight and feeding behaviour of bats: predicted mean (a) and minimum (b) flight speed, mean (c) and maximum (d) feeding buzz probability, and sinuosity (e) of trajectories at paired control and solar sites, from generalised linear mixed models, for bat guilds and species (MRE: mid-range echolocators; Pippyg: *P. pygmaeus*; Pippip: *P. pipistrellus*; Pipkuh: *P. kuhlii*; Pipnat: *P. nathusii*; Pleaus: *P. austriacus*; SRE: short-range echolocators). Only significant effects ($p < 0.05$) are represented, and vertical bars represent 95% confidence intervals.

them on the surface of the solar panels where aerial hawking bats (i.e. non-gleaning bats) are less able to capture them (Schnitzler & Kalko, 2001). Further studies could disentangle the effects of

changes in plant community traits and polarised light induced by solar panels on the availability and spatial distribution of nocturnal insect prey consumed by bats. Finally, as a last potential

TABLE 1 Effects of solar farms on the flight and feeding behaviour of bats: predicted values and associated 95% confidence intervals (in square brackets) of each feeding behaviour metric at solar and control sites, for each bat guild and species from generalised linear mixed models, and associated changes in these values at solar sites compared to control sites (MRE: mid-range echolocators; Pippyg: *Pipistrellus pygmaeus*; Pippip: *Pipistrellus pipistrellus*; Pipkuh: *Pipistrellus kuhlii*; Pipnat: *Pipistrellus nathusii*; Pleaus: *Plecotus austriacus*; SRE: short-range echolocators). Only significant effects ($p < 0.05$) are represented.

Response variable	Taxa	Predicted values [95% CI]		% of change at solar versus control sites
		Solar sites	Control sites	
Mean flight speed (m/s)	Mid-range echolocators	4.61 [4.08, 5.17]	4.16 [3.67, 4.68]	9.7
	<i>P. pygmaeus</i>	5.10 [4.75, 5.45]	3.85 [3.62, 4.09]	24.4
	<i>P. kuhlii</i>	5.75 [4.79, 6.79]	3.73 [3.13, 4.37]	35.1
	<i>P. nathusii</i>	4.41 [2.96, 5.86]	5.79 [4.33, 7.25]	-31.4
	Short-range echolocators	4.83 [3.87, 5.79]	3.98 [3.03, 4.94]	17.5
	<i>P. austriacus</i>	5.24 [4.40, 6.08]	3.48 [2.69, 4.27]	33.7
Minimum flight speed (m/s)	<i>P. kuhlii</i>	1.64 [1.20, 2.24]	0.95 [0.73, 1.25]	41.9
	<i>P. pygmaeus</i>	5.10 [4.75, 5.45]	3.85 [3.62, 4.09]	24.4
	Short-range echolocators	1.32 [1.12, 1.52]	1.06 [0.85, 1.26]	20.1
	<i>P. austriacus</i>	1.45 [0.97, 2.17]	0.81 [0.55, 1.21]	44.1
Mean buzz probability	Mid-range echolocators	0.024 [0.020, 0.028]	0.030 [0.025, 0.034]	-17.5
	<i>P. pipistrellus</i>	0.023 [0.015, 0.031]	0.038 [0.027, 0.050]	-39.4
	<i>P. nathusii</i>	0.017 [0.013, 0.020]	0.021 [0.017, 0.025]	-22.5
Maximum buzz probability	<i>P. pipistrellus</i>	0.095 [0.061, 0.129]	0.137 [0.010, 0.174]	-30.7
Sinuosity	Short-range echolocators	1.16 [0.91, 1.45]	1.72 [1.35, 2.21]	-32.7

mechanism, solar panels could add clutter to the foraging environment, which could impose structural (more objects) as well as acoustic (more echoes to interpret and reflections of echolocation calls) challenges to bats (Greif et al., 2017). However, future studies on this type of panel could combine three-dimensional acoustic tracking with high-resolution imagery methods to assess the effects of such potential sensory traps and their impact on prey capture success, and on the risk of collision and confusion with water surfaces for drinking.

The lower mean flight speed of *P. nathusii* at solar sites than at paired control sites is the only result that does not support our original hypothesis. Although we have no clear explanation for this result, the lower average buzz probability we found at solar sites does support the hypothesis and confirms that feeding habitat quality was reduced at solar sites for *P. nathusii*. In addition, the fact we did not detect differences in buzz probability between solar and control sites for taxa other than MRE and *Pipistrellus* spp. is not surprising, as these less common taxa had very low buzz rates, which decreases statistical power and prevents any effects from being detected (Schnitzler & Kalko, 2001).

The magnitude of behavioural change due to solar farms that we report is strong, which suggests a major loss of habitat feeding functionality for bats. We believe that this loss of functionality could contribute to a decrease in the quality of the landscape as perceived by bats and force them to travel greater distances to feed (Laforge

et al., 2021). However, these results do not inform us about the net consequences that this decreasing habitat quality may have on population dynamics. Indeed, it is difficult to quantify feeding loss accurately, since bats, especially gleaning species, do not always emit a feeding buzz when capturing an insect, and a feeding buzz does not always indicate a successful capture (Britton & Jones, 1999; Stidsholt et al., 2023; Surlykke et al., 2003). We were not able to carry out aerodynamic modelling, as we did not have morphological data for bat populations at the time and sites we sampled, so we were unable to assess whether the flight speeds we recorded at control sites were energetically optimal speeds. Consequently, we could not determine whether the increase in flight speed at photovoltaic sites represented a shift from optimal foraging to commuting flight (i.e. minimising energy expenditure per time for a given minimal power speed, or minimising it per distance for a given maximal range speed), or an intermediate suboptimal shift. In both cases, given the extent of the increase in flight speeds leading to a greater probability of commuting, it is very likely that the presence of solar panels resulted in additional energy costs for the individuals (Grodzinski et al., 2009; Norberg & Rayner, 1987). Finally, although the sites studied covered a large geographical area, sampling only spanned 9 days in September, so future studies should confirm these patterns in other seasons and bioclimatic areas.

Our results show that even development projects that do not require total sealing of the soil for building or paving can lead to reduced

habitat quality. The resulting functionality loss is a form of habitat loss for bats, which should be addressed in the context of the mitigation hierarchy, a well-established legal framework to counteract impacts of development projects on biodiversity, by (i) avoiding impacts (e.g. avoiding spatial locations where high impact is expected due to the abundance of food resources, such as wetlands), (ii) reducing impacts (e.g. limiting the land area used for solar farms) and, as a last resort, (iii) offsetting residual impacts on biodiversity (e.g. creating new habitats; Business and Biodiversity Offsets Programme (BBOP), 2012; Gardner et al., 2013). As the exact mechanisms triggering the effects we documented remain unknown, reduction levers seem to be limited, and efforts should thus be made firstly, to avoid using sites with the greatest feeding potential for bats as solar farms, and secondly, to offset the residual effects by improving the carrying capacity of the food web within and around solar farms development projects (Tölgyesi et al., 2023). For example, the composition of plant communities at solar farms could be improved by sowing native flowering plant species (Peter et al., 2021) by creating agroecological infrastructures, such as hedgerows and flower fields supporting insects (Froidevaux et al., 2019; Krings et al., 2022), or by livestock grazing providing dung-feeding insects and avoiding the need to cut and remove the vegetation (Zaplata, 2023), that are widely known to benefit feeding bats. In this way, the transition to renewable energy can continue while negative effects on bats are minimised.

AUTHOR CONTRIBUTIONS

Kévin Barré and Alice Baudouin designed the study and collected the data. Kévin Barré created the workflow for data preparation and processing. Kévin Barré conducted the analyses with the support of Christian Kerbiriou and Alice Baudouin. Kévin Barré led the writing of the manuscript with the input of Christian Kerbiriou, Jérémy S. P. Froidevaux, Alice Baudouin and Vivien Chartendraul.

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CONFLICT OF INTEREST STATEMENT

CNR is a developer of photovoltaic projects which partially funded the study, and did not influence the analyses, interpretations,

discussions and conclusions of the study. None of the authors was employed by any of the funders prior to, or at the time of the submission of the article. Authors declare having no other competing interest.

DATA AVAILABILITY STATEMENT

Data available via the Zenodo platform <https://doi.org/10.5281/zenodo.10149959> (Barré et al., 2023).

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SUPPORTING INFORMATION

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

Table S1. Solar farms where acoustic sampling for bats was carried out: summary of sampling dates, weather during field sessions, type of solar panel, and information about herbaceous vegetation, and landscape features for each pair sampled. Values are shown separately for control (C) and solar (S) sites of each pair. Wilcoxon signed rank tests show that the landscape composition did not significantly differ between control and treatment sites.

Table S2. Summary of the number of three-dimensional positions and trajectories recorded for each bat guild and species.

Table S3. Summary of the relationships (estimates, standard errors and *p*-values) between trajectory feeding buzz probability variables and flight behaviour metrics (mean and minimum flight speed and sinuosity) for each bat guild and species from generalised linear mixed models (***p* < 0.001; ***p* < 0.01; **p* < 0.05). *N* = the number of bat trajectories included in models.

Table S4. Estimates, standard errors and *p*-values of the effect of the presence of solar panels on feeding behaviour metrics for each bat guild and species from generalised linear mixed models (***p* < 0.001; ***p* < 0.01; **p* < 0.05).

Supporting Information S1. Computing imprecision of 3D positions and accounting for it in the modelling.

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