

1 Acoustic activity of bats at power lines correlates with relative humidity: a
2 potential role for corona discharges

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18

19 **Abstract**

20 With the ever-increasing dependency on electric power, electrical grid networks are expanding
21 worldwide. Bats exhibit a wide diversity of foraging and flight behaviours, and their sensitivity to
22 anthropogenic stressors suggests this group is very likely to be affected by power lines in a myriad of
23 ways. Yet the effects of power lines on bats remains unknown. Here we assessed the responses of
24 insectivorous bats to very high voltage power lines (>220 kV, VHVPL). We implemented a paired
25 sampling design and monitored bats acoustically at 25 pairs, one pair consisting of one forest edge near
26 to VHVPL matched with one control forest edge. Relative humidity mediates the effects of power lines
27 on bats: we detected bat attraction to VHVPL at high relative humidity levels and avoidance of VHVPL
28 by bats at low relative humidity levels. We argue that the former could be explained by insect attraction
29 to the light emitted by VHVPL due to corona discharges while the latter may be due to the physical
30 presence of pylons/cables at foraging height and/or because of electromagnetic fields. Our work
31 highlights the response of bats to power lines at foraging habitats, providing new insight into the
32 interactions between power lines and biodiversity.

33

34 **Keywords**

35 Chiroptera, corona effect, electromagnetic fields, foraging behaviour, light, noise.

36 **1. Introduction**

37 With the ever-increasing dependency on electric power in modern societies and the recent expanding
38 focus on electrification as part of climate change mitigations [1, 2], electrical grid networks are
39 expanding worldwide. Very high-voltage power lines (≥ 220 kV, VHVPL) traverse over 300,000 km in
40 Europe and the network is expected to grow further. In addition to collision and electrocutions [3, 4],
41 power lines may negatively affect biodiversity through various mechanisms, ranging from habitat loss
42 and fragmentation [5, 6] to the effects of electromagnetic fields [7, 8]. In contrast, some species may
43 benefit from the presence of power lines, possibly as a consequence of the altered environmental
44 conditions or the management conducted under power lines [9, 10]. To date, however, information on
45 the interactions between power lines and biodiversity remains largely limited to birds [5].

46 Because of the wide diversity of foraging and flight behaviours exhibited by bats [11] and their
47 sensitivity to anthropogenic stressors [12], this taxa is very likely to be affected (either negatively or
48 positively) by power lines in a myriad of ways. Large species, species flying at height of the wires
49 (typical height for VHVPL: ~10-50 m above ground, but varies with topography), and species foraging
50 in open habitats are the most susceptible to barrier effects from VHVPL, which include mortality by
51 collision and electrocution, and site avoidance. For instance, Tella, Hernández-Brito [13] recently
52 documented the electrocution of 300 Indian flying foxes (*Pteropus giganteus*) in Sri Lanka while
53 Kahnonitch, Lubin [14] revealed power line avoidance by the open-space and high-flying forager
54 *Tadarida teniotis* in Israel. Studies assessing the effects of forest logging (e.g. clearcutting) on bats also
55 indicate that habitat modification during the installation and maintenance of power lines could benefit
56 open- and edge-space specialists because of increased habitat availability [15, 16] but could also
57 negatively affect clutter-adapted species that mainly forage within forest.

58 Furthermore, bats could be affected by less perceptible abiotic impacts of power lines such as
59 corona discharges and electromagnetic fields. Corona discharge – an electric discharge produced by the
60 ionization of atmospheric air surrounding the conductors – mainly occurs during wet conditions
61 (relative humidity level >80 - 90%) with low wind speed (< 2 m/s) [17]. It results in the production of a

62 hissing noise (see power spectra and spectrograms of the hissing sounds in electronic supplementary
63 material S1) [18] and the emission of blue and ultraviolet light over the entire conductor all along the
64 span length (the spark generating these lights occurs at each voltage peak, i.e. ca. 100 times per second
65 in 50 Hz VHVPL with alternative current (AC)) and on insulators [19] (see spectral composition of
66 corona discharge emission in air in electronic supplementary material S1). Noise may disrupt bat
67 foraging behaviour and deter bats from approaching power lines either because of avoidance [20, 21],
68 noise-induced distraction [22] and/or auditory masking [23, 24]. Masking may be more pronounced in
69 species that rely on listening for prey-generated sounds to glean prey from substrates, especially if low
70 frequency noise overlaps with the frequency hearing sensitivity of the bats. In contrast, corona
71 discharges produce blue and UV light that can attract insects sensitive to these short wavelengths [25-
72 27]. Insect attraction may, in turn, attract ‘light tolerant’ insectivorous bats to power lines, as is the case
73 for streetlamps, especially those that emit short wavelength light [28]. Species that use magnetic cues
74 are particularly affected by EMF generated by power lines [29] and this is the case of many bat species
75 which use Earth’s magnetic fields for homing, roosting and foraging [30-32]. Power lines generate
76 extremely low frequency EMFs (50-60 Hz) but also EMFs at higher frequency (mainly between 150
77 kHz to 30 MHz) when corona discharges occur [33]. EMFs could exert avoidance responses in bats and
78 disrupt foraging behaviour as documented for other mammals [34] and as also observed in bats at the
79 much higher frequencies emitted by radar [35, 36] (but see [37]).

80 Since bats are expected to respond either positively or negatively to power lines depending on
81 foraging guild, the net effect of power lines on bat communities is not obvious and has not been
82 assessed. In this study, we examined the responses of insectivorous bats to VHVPL in the field. The
83 aim was to assess the potential effects of VHVPL on bat activity and foraging intensity while controlling
84 for the landscape context. We tested the hypothesis that bats would avoid power lines (i.e. lower bat
85 foraging activity at foraging habitats near power lines). Four potential non-exclusive mechanisms for
86 avoidance are (i) the physical presence of these structure (pylons and cables) at foraging height which
87 may affect high-flying species and open-space foragers; (ii) exposure to electromagnetic fields that may

88 disrupt foraging behaviour; (iii) noise caused by corona discharges, especially for passive-listening bats,
89 and/or (iv) corona light that may deter light-sensitive species due to high perceived predation risk (Table
90 1). We also tested a contrasting hypothesis that light emitted by VHVPL due to corona discharge would
91 attract light-tolerant bats to VHVPL (Table 1). More specifically, we predicted higher bat activity and
92 foraging intensity near VHVPL for light-tolerant bat species during wet conditions (i.e. when corona
93 discharges occur) because of insect aggregation. This is the first study we are aware of to examine the
94 response of bats to power lines, providing new insight into the interactions between power lines and
95 biodiversity.

96

97 **2. Methods**

98 *(a) Sampling design*

99 We applied a paired sampling design to investigate the effects of VHVPL on bat activity and foraging
100 intensity. The study was conducted in the Eastern part of France, in Doubs and Jura counties (electronic
101 supplementary material S1). We monitored bats between June and August (i.e. seasonal peak of bat
102 activity) at 25 pairs of sites over two years (2017: N=10; 2021: N=15). Each pair consisted of one forest
103 edge near to VHVPL (< 10 m; hereafter referred to as ‘treatment site’) matched with one control forest
104 edge (hereafter referred to as ‘control site’). Forest edges were adjacent to an agricultural field (pasture
105 or meadow). We selected forest edges as our sampling sites since they are used frequently as foraging
106 and commuting habitats for a wide range of bat species in the study area. Treatment and control sites
107 within each pair were matched at the local scale in terms of altitude and forest composition and at larger
108 scales in terms of landscape composition, configuration and diversity (electronic supplementary
109 material S2). We aimed at selecting pairs that were separated by a minimum distance of 1000 m from
110 each other (median of minimum distances between pairs: 2793 m, range: 972-7371 m). Sites within
111 pairs were separated by distances between 300 and 1500 m (median: 581 m). Control sites were at least
112 >200 m from any VHVPL (range: 241-981 m). Pairs were located along six aerial transmission AC
113 power lines, including one with maximum voltage of 225 kV (N=2 pairs) and five of 400 kV (N=23).

114 General information on electromagnetic field levels generated by power lines as well as sound
115 measurements and spectral emission of corona discharges can be found in electronic supplementary
116 material S1.

117

118 **(b) Acoustic analysis**

119 We sampled bats acoustically using SM2BAT+ recorders (sampling rate: 384 kHz; Wildlife Acoustics,
120 Concord, USA; electronic supplementary material S3). Sites within each pair were sampled
121 simultaneously during two to three consecutive nights, from 30 min before sunset to 30 min after
122 sunrise. We sampled between one and four pairs per night simultaneously, representing a total of 17
123 and 16 sampling nights in 2017 and 2021, respectively. Sampling took place during warm nights (>
124 10°C) with low wind speed (< 10 km/h) and no rain but with varying relative humidity levels, ranging
125 from 52 to 99% (electronic supplementary material S4). Weather conditions were retrieved from the
126 nearest weather station (<10 km; <https://www.meteociel.fr/>) and averaged over the entire night.

127 As the aim of the study was to assess the effects of VHVPL on both bat activity and foraging
128 intensity, we used bat sound recordings to calculate these response metrics. More specifically, we used
129 the number of bat passes recorded per night as a measure of bat activity and used the bat sequence
130 duration to get information on bat foraging intensity [38]. We defined a bat pass as one or more
131 echolocation calls recorded during a fixed interval of five seconds [39-41]. The fixed interval allowed
132 to standardize the measure of bat activity among bat species. A bat sequence duration was calculated as
133 the duration of a series of echolocation calls with interpulse intervals <2 s within one or several
134 consecutive bat passes of the same species or group of species (electronic supplementary material S5).

135 We automatically identified each bat pass to the lowest taxonomic level (i.e. species or species
136 group) using the *Tadarida* toolbox [42] which provides a confidence index associated to each bat
137 sequence identification. We then followed recommendations from Barré et al. Barré, Le Viol [41] to
138 account for potential automated identification errors. Thus, we used the confidence index to retain two
139 separate datasets: (i) one dataset of bat passes with a score ≥ 0.90 (i.e. with maximum error risk tolerance

140 of 10%); and (ii) another dataset of bat passes with a score ≥ 0.50 (i.e. with maximum error risk tolerance
141 of 50%). The former threshold is conservative and minimises the inclusion of false positives while the
142 latter is less cautious but retains a larger quantity of data. We conducted the statistical analyses on the
143 dataset of bat passes with a score ≥ 0.50 and checked for result consistency and robustness with the
144 other dataset [41].

145 We computed the community weighted mean bat sequence duration (CWMBSD) – a metric
146 related to foraging intensity at the bat community level – as follows:

147

$$148 \quad (1) \quad CWMBSD_j = \frac{\sum_{i=1}^n a_{ij} (MBSD_{ij})}{\sum_{i=1}^n a_{ij}}$$

149

150 where n is the total number of species or species group recorded, a_{ij} is the number of bat sequences of
151 the species or species group at a given site-night combination j , and $MBSD_{ij}$ is the mean bat sequence
152 duration of the species or species group at a given site-night combination j . Beforehand, a_{ij} and $MBSD_{ij}$
153 were scaled with minimum = 0 and maximum = 1 as these metrics are not directly comparable on their
154 original scales between species or species group (notably because detection and abundance vary among
155 species). Longer bat sequences (i.e. higher values of CWMBSD) would indicate that a bat is foraging
156 while shorter bat sequences would suggest that a bat is commuting [38]. The CWMBSD provided a
157 single metric that can inform about overall bat foraging intensity and that is not correlated with other
158 response variables such as bat activity (electronic supplementary material S6).

159

160 **(c) *Landscape analysis***

161 Landscape composition, configuration and diversity are key drivers of bat activity at local
162 scales [43-47]. We therefore included landscape variables in our models to control for residual
163 variations. Since bats respond to landscape variables at different spatial scales [43, 48], we created ten
164 buffers of 50, 100, 250, 500, 750, 1000, 2000, 3000, 4000, and 5000 m radii around each sampling site
165 using ArcGIS Desktop v10 (ESRI, Redlands, CA, USA). The large scales represent the mean maximum

166 daily foraging movement of European bat species [49] whereas the small ones allow us to describe the
167 near environment of the sampling sites. Within each buffer, we calculated the amount of deciduous
168 forest, coniferous forest, grassland, cropland and urban area (CES OSO land cover data 2018, 10 m
169 resolution), and computed the density of hedgerows and rivers (IGN BD Haie and BD Carthage,
170 respectively) and distance to the nearest river. We used the “landscapemetrics” R-package to calculate
171 the edge density (landscape configuration) and the Shannon diversity of habitats (landscape diversity).
172

173 *(d) Statistical analysis*

174 We conducted a series of (generalized) linear mixed-effect models (GLMMs; “glmmTMB” package)
175 to assess the effects of VHVPL on bat activity and foraging intensity. The eleven response variables
176 were the number of bat passes per night for species or group of species (i.e. species-specific bat activity
177 and composite bat activity, ten response variables), as well as the community weighted mean bat
178 sequence duration per night (i.e. bat foraging intensity, one response variable). Composite bat activity
179 refers to the inclusion of species-specific bat activity in a single model to investigate the overall
180 response of bats to VHVPL. Models for bat activity were fitted with a negative binomial error
181 distribution due to over-dispersion and coupled with a logit link function while models for bat foraging
182 intensity were fitted with a Gaussian distribution. We considered site identity nested within pair as
183 random effects because bats were surveyed for several nights and to account for the paired-sampling
184 design. Moreover, we followed recommendations from Oberpriller, de Souza Leite [50] and added the
185 sampling year as an additional random effect, except for CWMBSD because of model non-convergence
186 (whether sampling year was included as random or fixed effect). Species identity was added as a random
187 factor in models for composite bat activity to account for non-independence of observations
188 corresponding to the same species [51].

189 For each response variable we built 10 candidate models (including the null one). We
190 considered three blocks of variables (A: experiment, i.e. VHVPL vs control (categorical variable), B:
191 weather variables (continuous variables), C: landscape variables (continuous variables)) that we
192 included independently (A, B, C), in combination (A+B, A+C, B+C, A+B+C), or in interaction

193 (between blocks A and B only, i.e. $A*B$, $A*B+C$) into the models. More specifically, weather variables
194 (block B) comprised the mean temperature at night to account for its well-known positive effect on bat
195 (foraging) activity and relative humidity at night given that corona discharges occur at wet conditions
196 (relative humidity levels >80-90%) with low wind speed (< 7.2 km/h) [17]. Since bat sampling took
197 place in calm conditions (see section (b) Acoustic analysis and electronic supplementary material S2)
198 we did not consider wind speed as a covariate. Among the nine landscape variables computed at ten
199 spatial scales, only the two most informative ones at their most relevant scale were considered in block
200 C (see electronic supplementary material S7 for landscape variable selection). We only restrained this
201 selection to two landscape variables to avoid collinearity issues and model overparameterization. To
202 test the effects of corona discharges, we included the interaction between the experiment and relative
203 humidity into the models (interaction between blocks A and B). Thus, the full models were written as
204 follows:

205

206 (2) Composite bat activity \sim experiment (VHVPL *vs* control) * relative humidity +
207 temperature + landscape variable 1 + landscape variable 2 + 1|pairID/siteID + 1|year +
208 1|speciesID

209 (3) Species specific bat activity \sim experiment (VHVPL *vs* control) * relative humidity +
210 temperature + landscape variable 1 + landscape variable 2 + 1|pairID/siteID + 1|year

211 (4) CWMBSD \sim experiment (VHVPL *vs* control) * relative humidity + temperature +
212 landscape variable 1 + landscape variable 2 + 1|pairID/siteID

213

214 All continuous, explanatory variables were standardized prior to their inclusion within the full
215 models so that the regression coefficients were comparable in magnitude. We then applied an
216 information-theoretic approach using the $AICc$ to select the most parsimonious models [52] and
217 accounted for model uncertainty by computing model averaged predictions and standard errors across
218 best models ($\Delta AICc < 6$) [53-55]. We determined statistical significance using effect size statistics and

219 their confidence intervals (CIs) [56]. In line with Muff, Nilsen [57], we considered as weak, moderate
220 and strong evidence when the 85, 95 and 98% CIs did not overlap zero, respectively. We checked for
221 model assumptions, assessed collinearity among predictors and spatial autocorrelation of model's
222 residuals, and validated our models (see details in the electronic supplementary material S8).

223 Finally, when the interaction between the experiment and relative humidity was significant, we
224 tested the bat activity-relative humidity relationship at control sites, and at power line sites
225 independently, using the “emmeans” package (on the full model). From the same package, we then
226 conducted pairwise comparison of bat activity and foraging intensity between control and power line
227 sites at each extreme value of the relative humidity gradient sampled (i.e. at 52% and 98%) at which
228 we expect absence and presence of corona discharges, respectively. All analyses were conducted in R
229 v4.1.1 [58] and references of packages used are presented in the electronic supplementary material S9.

230

231 **3. Results**

232 ***(a) Bat sampling***

233 We recorded a total of 87,940 bat passes along 50 forest edges surveyed (117 detector-nights). The most
234 detected species (or species groups) were *Pipistrellus pipistrellus* with 68,360 bat passes (77.7% of the
235 total bat activity), followed by *Eptesicus serotinus* (7.7%), small *Myotis* bats (4.3%, hereafter referred
236 to as ‘*Myotis* spp.’ which includes *M. alcathoe*, *M. bechsteinii*, *M. brandtii*, *M. daubentonii*, *M.*
237 *emarginatus*, *M. mystacinus*, and *M. nattereri*), *Pipistrellus nathusii/kuhlii* (4.3%), *Pipistrellus*
238 *pygmaeus/Miniopterus schreibersii* (1.6%), *Barbastella barbastellus* (1.6%), *Nyctalus* spp. (1.6%),
239 *Rhinolophus hipposideros* (0.6%), and *Myotis myotis/blythii* (0.5%, large *Myotis* bats). We recorded
240 <100 bat passes of *Rhinolophus ferrumequinum* and *Plecotus* spp. and therefore disregarded these
241 species for the analysis.

242

243 ***(b) Effects of power lines on bat activity and foraging intensity***

244 We found evidence that eight out of the 11 response variables investigated in this study (i.e.
245 species-specific bat activity, composite bat activity and CWMBSD, a metric related to foraging
246 intensity at the bat community level) responded to VHVPL. For each response variable, between three
247 and ten models were considered as best models after model selection. The null model was, however,
248 retained amongst best models for *Myotis* spp. activity, composite bat activity and CWMBSD (electronic
249 supplementary material S10).

250 The interaction between the experiment (VHVPL vs control) and mean relative humidity at
251 night was retained in all sets of best candidate models after model selection (electronic supplementary
252 material S10). Our models revealed a significant interaction (with varying strength of evidence)
253 between mean relative humidity at night and the presence of power lines on bats for 7 out 11 of our
254 response variables (Table 2). Overall, there was lower bat activity and CWMBSD at control sites with
255 increasing relative humidity, but at power line sites these relationships were stable or even positive.
256 This general pattern was especially supported by our results on *B. barbastellus* and *P. pipistrellus*
257 activity, composite bat activity and CWMBSD (Figure 1; electronic supplementary materials S11 and
258 S12) as well as on *E. serotinus*, *M. myotis/blythii* and *P. pygmaeus/M. schreibersii* activity, though only
259 with weak support (Table 2, Figure 2, electronic supplementary material S12).

260 The pairwise comparison of bat activity and CWMBSD between control sites and power lines
261 at the extreme values of the relative humidity gradient further indicated that relative humidity mediates
262 the effects of power lines on bats. For a low relative humidity level (here 52%) at which no corona
263 discharges are expected we found avoidance of power lines by bats – i.e. lower bat activity and
264 CWMBSD at power lines compared to control sites (Figure 3). Conversely, for a high relative humidity
265 level (here 98%) at which corona discharges occur, we found bat attraction to power lines with higher
266 activity CWMBSD at power lines compared to control sites (Figure 3). This general pattern was
267 detected for most response variables but with varying strength of evidence (Figure 3).

268 Furthermore, we found moderate evidence that *Nyctalus* spp. activity was negatively affected
269 by the presence of very high voltage power lines (Table 2, Figure 4), irrespective of meteorological

270 conditions. *Nyctalus* spp. activity was almost twofold lower (i.e. 46% reduction) at forest edges located
271 near power lines compared to matched control sites. No evidence for an effect of power lines on *Myotis*
272 spp., *P. nathusii/kuhlii*, and *R. hipposideros* activity was detected (Table 2).

273 Finally, when comparing model outputs between the two bat datasets (i.e. datasets with acoustic
274 data identified at the 50% and 10% error risk tolerance, respectively), influential variables showed
275 consistent patterns (electronic supplementary material S13). We are therefore confident in our results
276 as they are not sensitive to the rate of error risk tolerance.

277

278 ***(c) Effects of landscape variables on bat activity and foraging intensity***

279 Landscape variables were retained in all most parsimonious models (electronic supplementary
280 material S9) and had significant effects on species-specific bat activity but no effect on CWMBSD (a
281 metric related to foraging intensity at the bat community level) and composite bat activity (electronic
282 supplementary material S13). The effect of landscape compositional heterogeneity (i.e. Shannon
283 diversity of habitats) at broad spatial scale (≥ 2 km radius scale) was always positively associated with
284 bat activity, including *E. serotinus*, *M. myotis/blythii*, *P. nathusii/kuhlii*, and *P. pipistrellus*. The density
285 of hedgerows was the most selected landscape variable in models on species-specific bat activity
286 (present in six out of nine models) but had contrasting effects: the activity of *B. barbastellus*, *R.*
287 *hipposideros*, and *P. pygmaeus/M. schreibersii* increased with hedgerow density while the opposite was
288 true for *M. myotis/blythii* and *Nyctalus* spp. and no significant effect was found for *Myotis* spp.
289 Additionally, the amount of coniferous forest at 4 km radius scale had a negative effect on both *B.*
290 *barbastellus* and *P. pipistrellus nathusii/kuhlii* activity whereas *R. hipposideros* was less active with
291 increasing deciduous forest cover at the small spatial scale (50 m radius scale). The density of river at
292 5 km radius scale was positively related with the activity *P. pipistrellus* and *P. pygmaeus/M.*
293 *schreibersii*. Surprisingly, grassland cover had negative effects on open-space forager activity (*E.*
294 *serotinus* and *Nyctalus* spp.).

295

296 **4. Discussion**

297 Our field experiment shows conclusively that bat activity and foraging intensity at foraging
298 habitats are affected by the presence of very high voltage power lines (VHVPL). Overall, our results
299 indicate that relative humidity mediates the effects of power lines on bats as we detected bat attraction
300 to power lines at high relative humidity levels (i.e. when corona discharges occur) and avoidance of
301 power lines by bats at low relative humidity levels (i.e. when no corona discharges are expected). While
302 the underlying mechanisms remain to be tested, the former result is consistent with expectations from
303 our hypothesis that light emitted by VHVPL due to corona discharges would attract insects and therefore
304 increase bat foraging intensity near VHVPL. From the four potential non-exclusive mechanisms that
305 could explain power line avoidance by bats, our results suggest that any negative effects of VHVPL on
306 bats are most likely due to the physical presence of the power lines and/or exposure to extremely low
307 frequency electromagnetic fields. Noise, light and high frequency EMFs arising from corona discharges
308 seemed to play no role in explaining avoidance of power lines by bats.

309 We found that relative humidity exacerbated bat activity and community-level foraging
310 intensity at foraging habitats near power lines compared to control sites. Among many other factors,
311 corona discharges at power lines mainly occur during wet conditions [17] and result in the emission of
312 UV and blue light with peaks within the range of 230-440 nm [19]. The so-called ‘corona light’ has
313 shown to be responsible of power lines avoidance by reindeer [59], but given its spectrum it may attract
314 nocturnal insects [25, 26] and thus bats. Interestingly, we found attraction to power lines in both light-
315 tolerant (e.g. *P. pipistrellus*) and light-sensitive (e.g. *B. barbastellus*) bat species and no attraction or
316 avoidance in other light-sensitive bats present in our study area including species (e.g. *Myotis* spp.) that
317 may perceive UV and short wavelength blue light [60, 61]. While we did not specifically test the corona
318 effect on insect prey, previous studies have highlighted clear positive relationships between insect
319 abundance and bat (foraging) activity [62-64]. Furthermore, our results not only suggest changes in bat
320 activity but also changes in bat behaviour with increased foraging intensity near power lines when
321 corona discharges occur (i.e. at high relative humidity levels), thus implying that changes in bat activity

322 mirror bat responses to their insect prey. Direct measurements of insect abundance in relation to corona
323 discharges are however needed to confirm the process involved. Indeed, other factors such as high
324 frequency EMFs due to corona discharges could also be at play (e.g. by disrupting sensory orientation
325 of bats), but so far the only studies assessing the effects of electromagnetic fields on bats have suggested
326 either a negative effect on bat activity and foraging intensity [35, 36] or no impact [37], albeit at much
327 higher frequencies. Further research is also required to identify the distance at which this cascading
328 effect operates to fully appreciate the mechanisms involved.

329 Corona discharges can also cause a hissing noise and we predicted power lines avoidance by
330 passive-listening bats – here *Myotis myotis/blythii* [65] and *Plecotus* spp. [66] – during wet conditions.
331 We could not test this hypothesis with *Myotis* spp. in a robust way as this species group includes both
332 active- (e.g. *M. nattereri*) and passive- (e.g. *M. bechsteini*) listening bat species [67], even though the
333 former is more likely to forage at forest edges than the later. However, our results on *M. myotis/blythii*
334 refute the power lines avoidance hypothesis due to “noise disruption” since its activity at forest edges
335 near power lines was less affected by relative humidity compared to control sites. We did not have
336 enough records of *Plecotus* spp. to conduct the analysis on its activity or occurrence and the potential
337 effects of noise produced by VHVPL on this species group cannot be excluded for two reasons. First,
338 *Plecotus* spp. cease echolocating during the hovering phase of gleaning attacks [68] and are therefore
339 more likely to be disrupted by noise. Second, *Plecotus* spp. have exceptionally high hearing sensitivity
340 with a threshold of -20 dB sound pressure level for hearing frequencies between 12-19 kHz [69], i.e. in
341 the high frequency range of sound produced by the power lines.

342 Our prediction on power line avoidance by high-flying and open-space foragers due to the
343 physical structure (pylons and cables) of the power lines was supported by our results on *Nyctalus* spp.
344 which showed significantly higher activity at control sites than near VHVPL regardless of the weather
345 conditions. The *Nyctalus* species group includes *N. noctula* and *N. leisleri*, two open-space forager
346 species that forage at height [70]. Our results for *Nyctalus* spp. corroborates those of Kahnonitch, Lubin
347 [14] who revealed that the activity of the open-space and high-flying forager *T. teniotis* decreases closer

348 to 161 KV power lines. Overhead wires greatly vary in height depending on topography (from 10 m to
349 >50 m, especially in our hilly study area) and may overlap with the flight height of *Nyctalus* spp., thus
350 potentially representing obstacles while foraging/commuting.

351 However, we also observed power line avoidance by other bat species (*B. barbastellus*, *E.*
352 *serotinus*, *P. pipistrellus*, and *P. pygmaeus/M. schreibersii*) and reduced composite activity and
353 foraging intensity at power lines, but only at low relative humidity levels. Wing morphology of these
354 bat species makes them more manoeuvrable than *Nyctalus* spp. [11] and it seems unlikely that overhead
355 wires represent physical barriers to movement for these species. As our sampling design does not
356 disentangle the effects of extremely low frequency electromagnetic fields (50 Hz) generated by the
357 VHVPL and the physical presence of VHVPL on bats, the potential negative effect of electromagnetic
358 fields on bats cannot be excluded. The mechanisms underlying the avoidance of power lines by bats
359 merits further investigation and further behavioural experiments are therefore needed to assert our
360 findings.

361 To conclude, our work highlights the response of bats to power lines at foraging habitats,
362 providing new insight into the interactions between power lines and biodiversity. We found that the
363 effects of VHVPL on bats results from a range of potential mechanisms, with (i) corona discharges
364 being one of the most likely factors responsible for bat attraction to power lines and (ii) the physical
365 presence of power lines and extremely low frequency electromagnetic fields generated by power lines
366 the main reasons explaining power lines avoidance by bats. VHVPL traverse over 300,000 km in Europe
367 and power lines avoidance by bats could result in large-scale loss, alteration and fragmentation of
368 foraging habitat, as observed with other anthropogenic structures [71-74]. This is especially true in more
369 arid areas where bats will not benefit from potential insect aggregation near power lines. Given that
370 power lines can have significant conservation consequences for these protected species in Europe, these
371 infrastructures should be considered in appropriate planning legislation and policy. We therefore
372 highlight the crucial need of mitigating any negative impact that power lines may cause to bats in arid
373 areas by applying the mitigation hierarchy with the ambition of no-net-loss, for instance by avoiding

374 siting new power lines near important foraging habitats and offsetting habitat loss (e.g. by
375 restoring/creating new habitats) caused by existing power lines.

376

377 **Ethics**

378 Ethical approval was given by University of Stirling Biological and Environmental Sciences Ethical
379 Committee.

380

381 **Data accessibility**

382 Data collected for this study and codes will be available to download on Zenodo. For the review
383 process, data and codes have been uploaded as part of the supplementary material. Acoustic
384 recordings are archived and available via the French citizen science programme “Vigie-Chiro”
385 (<http://vigienature.mnhn.fr/page/participer-vigie-chiro>), at the portal <http://vigiechiro.herokuapp.com/>.

386

387 **Authors' contributions**

388 JSPF secured the funding, designed the set-up of the study, collected, processed and analysed the data
389 and wrote the initial draft of the manuscript. KP and GJ supervised the project. CK developed the
390 CWMBSD equation. All authors contributed critically to the final version of the manuscript.

391

392 **Competing interests**

393 We declare we have no competing interests.

394

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398

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- 588

589 **Table 1.** Summary of a priori hypotheses regarding the potential effects of very high voltage power
590 lines on bats investigated in this study. (+) indicates positive association expected, and (–) negative
591 association.

Potential effects investigated	Expected responses
Physical presence of power lines (pylons and cables)	High-flying and open-space species (–)
Electromagnetic fields	All species (–)
Corona discharges: noise	Passive-listening species (–)
Corona discharges: light	Light-tolerant species (+) Light-sensitive species (–)

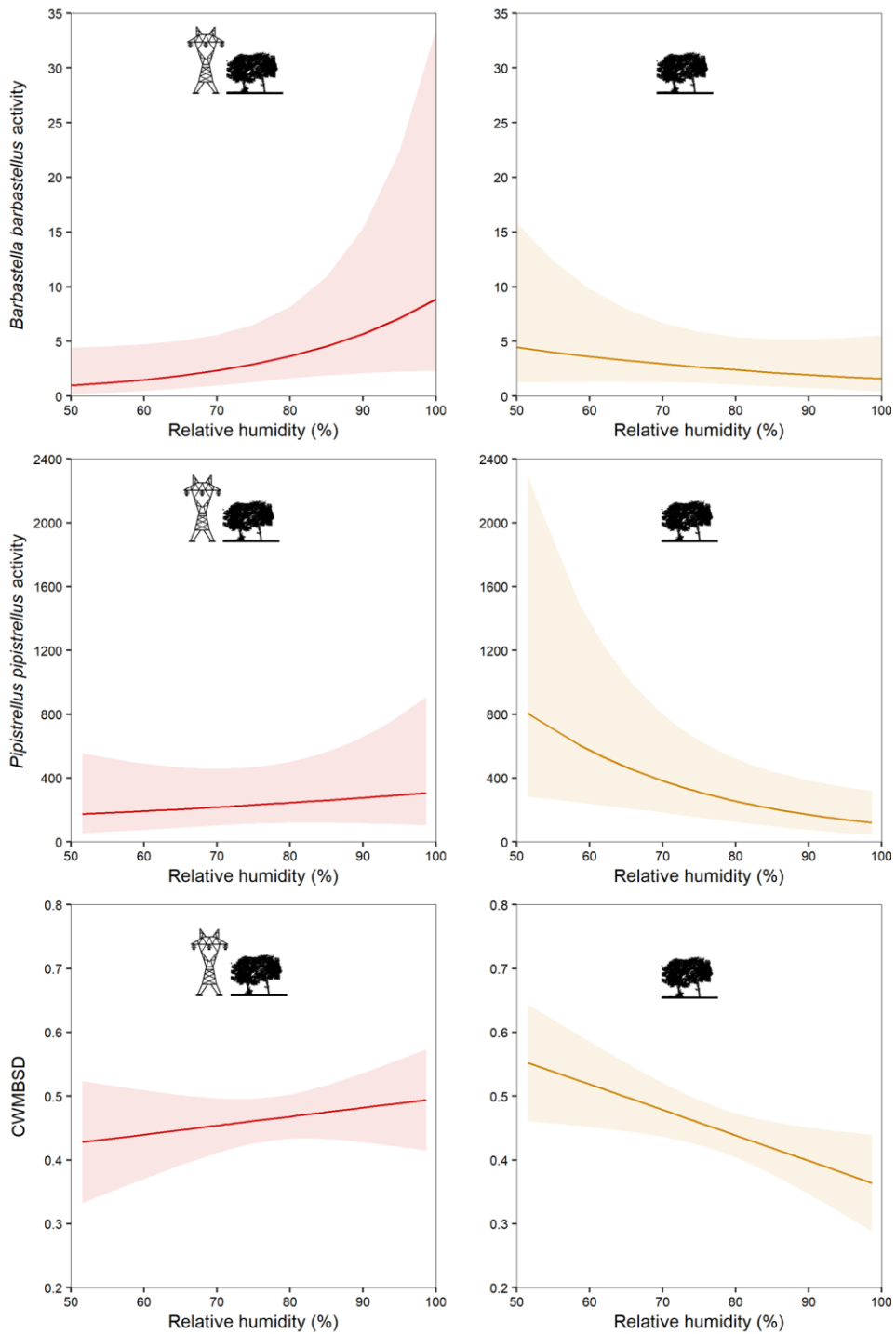
592

593 **Table 2.** Standardized, model-averaged parameter estimates with associated standards errors (SE) and 85, 95% and 98% confidence intervals (CIs) of the best
594 (G)LMMs ($\Delta AIC_c < 6$) relating the effects of very high voltage power lines, humidity, and their interaction on bat taxon-specific activity, composite bat activity
595 and community weighted mean bat sequence duration (CWMBSD). CIs that do not overlap zero are represented in bold red (85% CI: weak evidence; 95% CI:
596 moderate evidence; 98% CI: strong evidence). Description of the most parsimonious models can be found in electronic supplementary material S10 and full
597 results of the models in the electronic supplementary material S12.

598

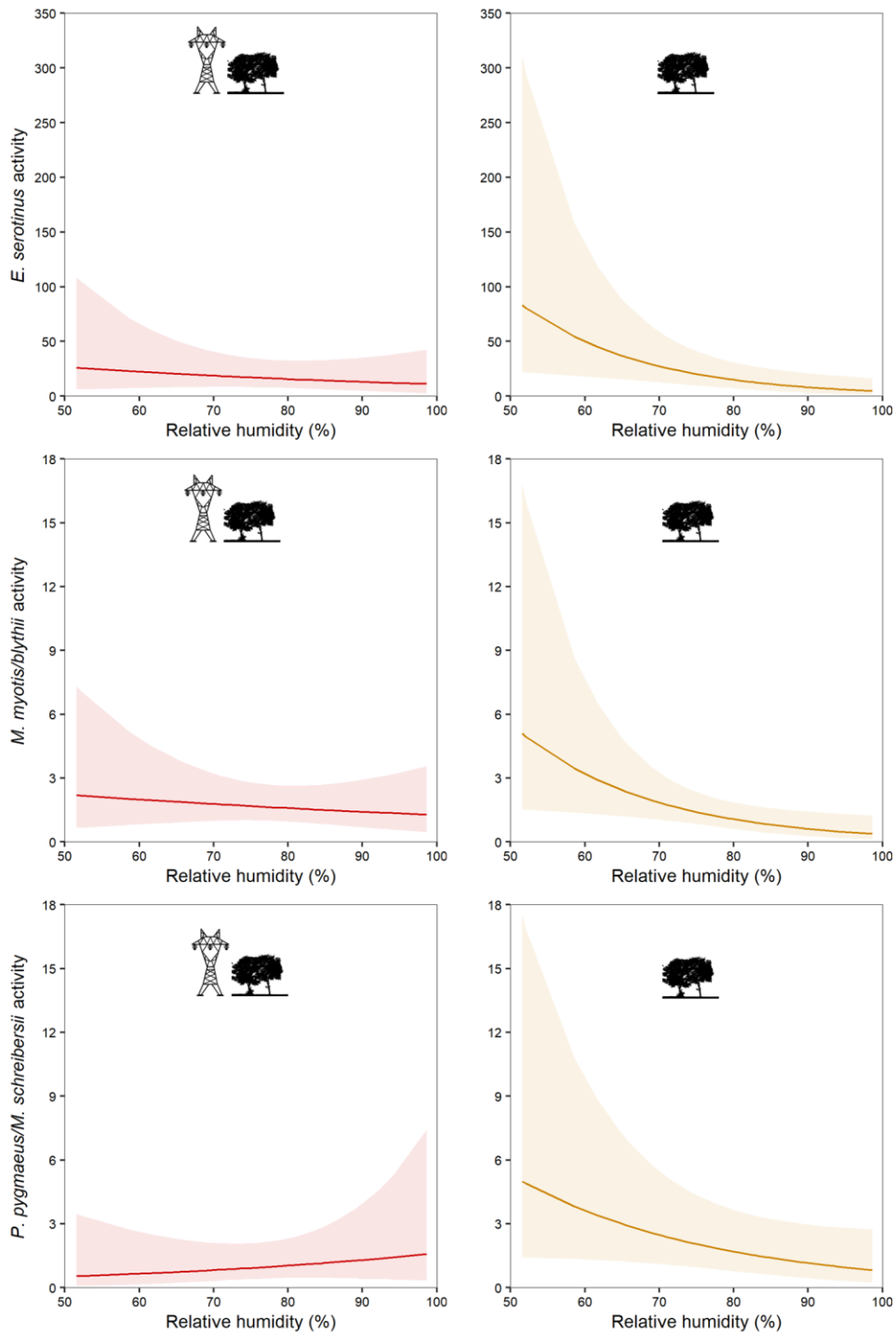
Variable		<i>Barbastella barbastellus</i>	<i>Eptesicus serotinus</i>	<i>Myotis myotis blythii</i>	<i>Myotis</i> spp.	<i>Nyctalus</i> spp.	<i>Pipistrellus nahuusii/kahlii</i>	<i>Pipistrellus pipistrellus</i>	<i>Pipistrellus pygmaeus /Miniopterus schreibersii</i>	<i>Rhinolophus hipposideros</i>	Composite bat activity	CWMBSD
Power line vs control	Est. ± SE	0.31 ± 0.31	-0.05 ± 0.30	0.29 ± 0.32	-0.05 ± 0.36	-0.63 ± 0.28	0.41 ± 0.35	-0.16 ± 0.30	-0.61 ± 0.46	0.39 ± 0.43	-0.25 ± 0.21	0.02 ± 0.03
	85% CI	-0.13, 0.75	-0.48, 0.39	-0.18, 0.75	-0.56, 0.46	-1.03, -0.22	-0.10, 0.92	-0.60, 0.28	-1.26, 0.05	-0.22, 1.01	-0.55, 0.05	-0.02, 0.05
	95% CI	-0.29, 0.91	-0.64, 0.55	-0.35, 0.92	-0.75, 0.65	-1.18, -0.08	-0.29, 1.10	-0.76, 0.44	-1.5, 0.29	-0.45, 1.23	-0.66, 0.16	-0.03, 0.07
	98% CI	-0.41, 1.03	-0.76, 0.66	-0.47, 1.04	-0.88, 0.78	-1.28, 0.03	-0.42, 1.24	-0.88, 0.56	-1.67, 0.46	-0.61, 1.39	-0.74, 0.24	-0.04, 0.08
Relative humidity	Est. ± SE	-0.18 ± 0.25	-0.53 ± 0.24	-0.41 ± 0.24	0.05 ± 0.15	0.32 ± 0.20	-0.41 ± 0.23	-0.38 ± 0.19	-0.35 ± 0.24	0.11 ± 0.22	-0.17 ± 0.13	-0.03 ± 0.02
	85% CI	-0.53, 0.18	-0.88, -0.18	-0.76, -0.06	-0.17, 0.28	0.03, 0.61	-0.75, -0.08	-0.66, -0.10	-0.69, 0.00	-0.20, 0.42	-0.36, 0.03	-0.06, 0.00
	95% CI	-0.66, 0.31	-1.00, -0.05	-0.89, 0.07	-0.25, 0.36	-0.08, 0.72	-0.87, 0.05	-0.76, 0.00	-0.82, 0.12	-0.32, 0.54	-0.43, 0.10	-0.07, 0.01
	98% CI	-0.75, 0.40	-1.09, 0.04	-0.98, 0.16	-0.30, 0.41	-0.16, 0.80	-0.96, 0.13	-0.83, 0.07	-0.90, 0.21	-0.40, 0.62	-0.48, 0.15	-0.08, 0.02
Power line vs control : Relative humidity	Est. ± SE	0.73 ± 0.29	0.48 ± 0.29	0.49 ± 0.31	0.19 ± 0.26	-0.26 ± 0.26	0.39 ± 0.30	0.59 ± 0.22	0.68 ± 0.36	0.34 ± 0.32	0.44 ± 0.16	0.06 ± 0.02
	85% CI	0.32, 1.14	0.06, 0.89	0.05, 0.93	-0.19, 0.56	-0.64, 0.11	-0.03, 0.82	0.25, 0.92	0.17, 1.20	-0.12, 0.80	0.22, 0.67	0.03, 0.10
	95% CI	0.17, 1.29	-0.10, 1.05	-0.12, 1.09	-0.33, 0.70	-0.78, 0.25	-0.19, 0.97	0.12, 1.05	-0.02, 1.39	-0.29, 0.97	0.13, 0.75	0.01, 0.11
	98% CI	0.06, 1.40	-0.20, 1.16	-0.23, 1.21	-0.43, 0.80	-0.88, 0.35	-0.30, 1.08	0.04, 1.13	-0.16, 1.52	-0.41, 1.09	0.08, 0.81	0.00, 0.12

599



600

601 **Figure 1.** Predicted bat responses with the 95% confidence interval to relative humidity at forest edges
 602 along very high voltage power lines (≥ 220 kV, VHVPL) (left hand panels, red) and control sites (right
 603 hand panels, orange). Predictions were obtained from models in which the interaction between the
 604 experiment (VHVPL vs control) and relative humidity was significant with **98% CI** around the estimate
 605 not overlapping zero. Activity: number of bat passes per night. CWMBSD: community weighted mean
 606 bat sequence duration (s).

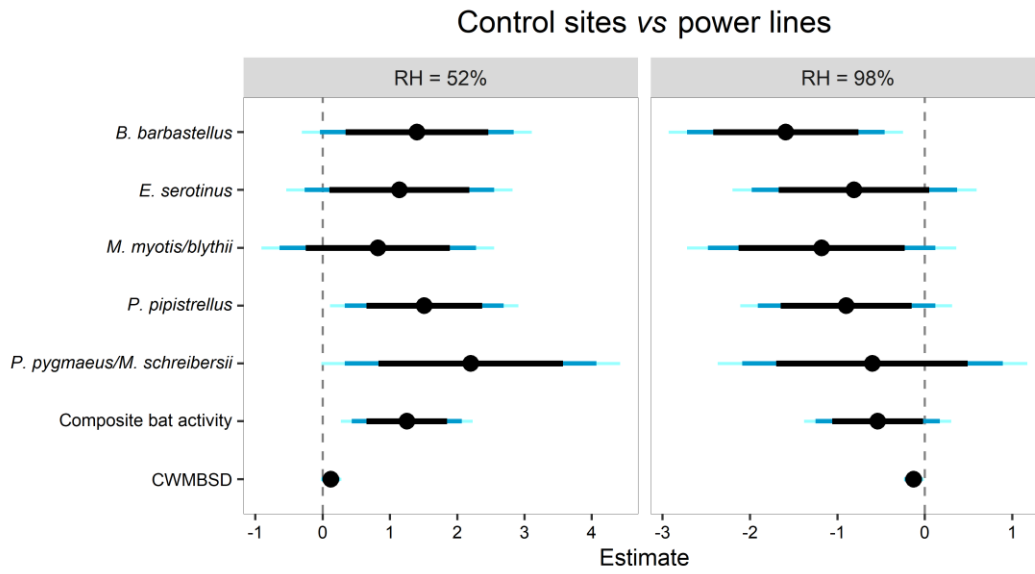


607

608 **Figure 2.** Predicted bat responses with the 95% confidence interval to relative humidity at forest edges
 609 along very high voltage power lines (≥ 220 kV, VHVPL) (left hand panels, red) and control sites (right
 610 hand panels, orange). Predictions were obtained from models in which the interaction between the
 611 experiment (VHVPL vs control) and relative humidity was significant with **85% CI** around the estimate
 612 not overlapping zero. Activity: number of bat passes per night.

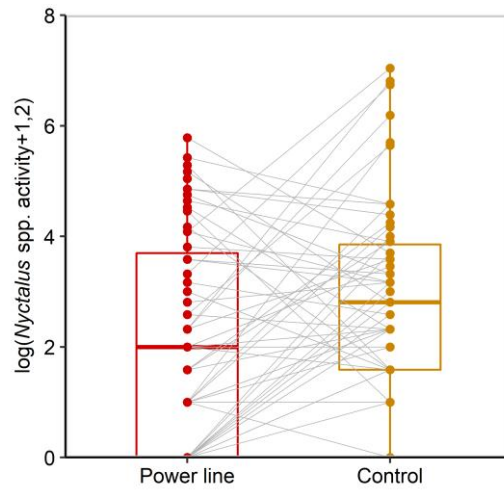
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616 **Figure 3.** Pairwise comparisons of bat activity and foraging intensity (CWMBSD) between control sites
617 and power lines at each extreme value of the relative humidity gradient sampled (i.e. 52 and 98%).
618 Estimates and associated 85%, 95% and 98% confidence intervals of the comparisons are represented
619 with black points and black, dark-blue and light-blue bars, respectively. Positive estimates indicate
620 higher bat activity and increased foraging intensity at control sites compared to power lines.



621

622 **Figure 4.** Boxplot of *Nyctalus* spp. activity (number of bat passes per night on a logarithm scale to the
 623 base 2) recorded at forest edges along very high voltage power lines (≥ 220 kV) and control sites. Dots
 624 represent raw data with paired sites and nights linked with a grey line. The boxplots display the
 625 interquartile range box (top line = 75% of the data \leq this value; middle line = median; lower line = 25%
 626 of the data \leq this value) and the lower and upper whiskers (minimum and maximum data points).

627