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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
26 near to VHVPL matched with one control forest edge. Relative humidity mediates the effects of
27 power lines on bats: we detected bat attraction to VHVPL at high relative humidity levels and
28 avoidance of VHVPL by bats at low relative humidity levels. We argue that the former could be
29 explained by insect attraction to the light emitted by VHVPL due to corona discharges while the latter
30 may be due to the physical presence of pylons/cables at foraging height and/or because of
31 electromagnetic fields. Our work highlights the response of bats to power lines at foraging habitats,
32 providing new insight into the 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
40 in Europe and the network is expected to grow further. In addition to collision and electrocutions [3,
41 4], power lines may negatively affect biodiversity through various mechanisms, ranging from habitat
42 loss and fragmentation [5, 6] to the effects of electromagnetic fields [7, 8]. In contrast, some species
43 may 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
47 their sensitivity to anthropogenic stressors [12], this taxa is very likely to be affected (either
48 negatively or positively) by power lines in a myriad of ways. Large species, species flying at height of
49 the wires (typical height for VHVPL: ~10-50 m above ground, but varies with topography), and
50 species foraging in open habitats are the most susceptible to barrier effects from VHVPL, which
51 include mortality by collision and electrocution, and site avoidance. For instance, Tella, Hernández-
52 Brito [13] recently documented the electrocution of 300 Indian flying foxes (*Pteropus giganteus*) in
53 Sri Lanka while Kahnnonitch, Lubin [14] revealed power line avoidance by the open-space and high-
54 flying forager *Tadarida teniotis* in Israel. Studies assessing the effects of forest logging (e.g.
55 clearcutting) on bats also indicate that habitat modification during the installation and maintenance of
56 power lines could benefit open- and edge-space specialists because of increased habitat availability
57 [15, 16] but could also 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
60 the 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
65 second in 50 Hz VHVPL with alternative current (AC)) and on insulators [19] (see spectral
66 composition of corona discharge emission in air in electronic supplementary material S1). Noise may
67 disrupt bat foraging behaviour and deter bats from approaching power lines either because of
68 avoidance [20, 21], noise-induced distraction [22] and/or auditory masking [23, 24]. Masking may be
69 more pronounced in species that rely on listening for prey-generated sounds to glean prey from
70 substrates, especially if low frequency noise overlaps with the frequency hearing sensitivity of the
71 bats. In contrast, corona discharges produce blue and UV light that can attract insects sensitive to
72 these short wavelengths [25-27]. Insect attraction may, in turn, attract 'light tolerant' insectivorous
73 bats to power lines, as is the case for streetlamps, especially those that emit short wavelength light
74 [28]. Species that use magnetic cues are particularly affected by EMF generated by power lines [29]
75 and this is the case of many bat species which use Earth's magnetic fields for homing, roosting and
76 foraging [30-32]. Power lines generate extremely low frequency EMFs (50-60 Hz) but also EMFs at
77 higher frequency (mainly between 150 kHz to 30 MHz) when corona discharges occur [33]. EMFs
78 could exert avoidance responses in bats and disrupt foraging behaviour as documented for other
79 mammals [34] and as also observed in bats at the much higher frequencies emitted by radar [35, 36]
80 (but see [37]).

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

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

97

98 **2. Methods**

99 *(a) Sampling design*

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

118

119 **(b) Acoustic analysis**

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

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

138 We automatically identified each bat pass to the lowest taxonomic level (i.e. species or
139 species group) using the *Tadarida* toolbox [42] which provides a confidence index associated to each
140 bat sequence identification. We then followed recommendations from Barré et al. Barré, Le Viol [41]
141 to account for potential automated identification errors. Thus, we used the confidence index to retain
142 two separate datasets: (i) one dataset of bat passes with a score ≥ 0.90 (i.e. with maximum error risk
143 tolerance of 10%); and (ii) another dataset of bat passes with a score ≥ 0.50 (i.e. with maximum error
144 risk tolerance of 50%). The former threshold is conservative and minimises the inclusion of false

145 positives while the latter is less cautious but retains a larger quantity of data. We conducted the
146 statistical analyses on the dataset of bat passes with a score ≥ 0.50 and checked for result consistency
147 and robustness with the other dataset [41].

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

150

151 (1)
$$CWMBSD_j = \frac{\sum_{i=1}^n a_{ij} (MBSD_{ij})}{\sum_{i=1}^n a_{ij}}$$

152

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

163

164 (c) *Landscape analysis*

165 Landscape composition, configuration and diversity are key drivers of bat activity at local
166 scales [43-47]. We therefore included landscape variables in our models to control for residual
167 variations. Since bats respond to landscape variables at different spatial scales [43, 48], we created
168 ten buffers of 50, 100, 250, 500, 750, 1000, 2000, 3000, 4000, and 5000 m radii around each sampling
169 site using ArcGIS Desktop v10 (ESRI, Redlands, CA, USA). The large scales represent the mean
170 maximum daily foraging movement of European bat species [49] whereas the small ones allow us to
171 describe the near environment of the sampling sites. Within each buffer, we calculated the amount of

172 deciduous forest, coniferous forest, grassland, cropland and urban area (CES OSO land cover data
173 2018, 10 m resolution), and computed the density of hedgerows and rivers (IGN BD Haie and BD
174 Carthage, respectively) and distance to the nearest river. We used the “landscapemetrics” R-package
175 to calculate the edge density (landscape configuration) and the Shannon diversity of habitats
176 (landscape diversity).

177

178 *(d) Statistical analysis*

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

194 For each response variable we built 10 candidate models (including the null one). We
195 considered three blocks of variables (A: experiment, i.e. VHVPL vs control (categorical variable), B:
196 weather variables (continuous variables), C: landscape variables (continuous variables)) that we
197 included independently (A, B, C), in combination (A+B, A+C, B+C, A+B+C), or in interaction
198 (between blocks A and B only, i.e. A*B, A*B+C) into the models. More specifically, weather
199 variables (block B) comprised the mean temperature at night to account for its well-known positive

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

210

211 (2)

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

214 (3) Species specific bat activity \sim experiment (VHVPL *vs* control) * relative humidity +

215 temperature + landscape variable 1 + landscape variable 2 + 1|pairID/siteID + 1|year

216 (4) CWMBSD \sim experiment (VHVPL *vs* control) * relative humidity + temperature +

217 landscape variable 1 + landscape variable 2 + 1|pairID/siteID

218

219 All continuous, explanatory variables were standardized prior to their inclusion within the
220 full models so that the regression coefficients were comparable in magnitude. We then applied an
221 information-theoretic approach using the $AICc$ to select the most parsimonious models [52] and
222 accounted for model uncertainty by computing model averaged predictions and standard errors across
223 best models ($\Delta AICc < 6$) [53-55]. We determined statistical significance using effect size statistics and
224 their confidence intervals (CIs) [56]. In line with Muff, Nilsen [57], we considered as weak, moderate
225 and strong evidence when the 85, 95 and 98% CIs did not overlap zero, respectively. We checked for

226 model assumptions, assessed collinearity among predictors and spatial autocorrelation of model's
227 residuals, and validated our models (see details in the electronic supplementary material S8).

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

235

236 **3. Results**

237 ***(a) Bat sampling***

238 We recorded a total of 87,940 bat passes along 50 forest edges surveyed (117 detector-nights). The
239 most detected species (or species groups) were *Pipistrellus pipistrellus* with 68,360 bat passes (77.7%
240 of the total bat activity), followed by *Eptesicus serotinus* (7.7%), small *Myotis* bats (4.3%, hereafter
241 referred to as ‘*Myotis* spp.’ which includes *M. alcaethoe*, *M. bechsteinii*, *M. brandtii*, *M. daubentonii*,
242 *M. emarginatus*, *M. mystacinus*, and *M. nattereri*), *Pipistrellus nathusii/kuhlii* (4.3%), *Pipistrellus*
243 *pygmaeus/Miniopterus schreibersii* (1.6%), *Barbastella barbastellus* (1.6%), *Nyctalus* spp. (1.6%),
244 *Rhinolophus hipposideros* (0.6%), and *Myotis myotis/blythii* (0.5%, large *Myotis* bats). We recorded
245 <100 bat passes of *Rhinolophus ferrumequinum* and *Plecotus* spp. and therefore disregarded these
246 species for the analysis.

247

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

249 We found evidence that eight out of the 11 response variables investigated in this study (i.e.
250 species-specific bat activity, composite bat activity and CWMBSD, a metric related to foraging
251 intensity at the bat community level) responded to VHVPL. For each response variable, between three
252 and ten models were considered as best models after model selection. The null model was, however,

253 retained amongst best models for *Myotis* spp. activity, composite bat activity and CWMBSD
254 (electronic supplementary material S10).

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

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

273 Furthermore, we found moderate evidence that *Nyctalus* spp. activity was negatively affected
274 by the presence of very high voltage power lines (Table 2, Figure 4), irrespective of meteorological
275 conditions. *Nyctalus* spp. activity was almost twofold lower (i.e. 46% reduction) at forest edges
276 located near power lines compared to matched control sites. No evidence for an effect of power lines
277 on *Myotis* spp., *P. nathusii/kuhlii*, and *R. hipposideros* activity was detected (Table 2).

278 Finally, when comparing model outputs between the two bat datasets (i.e. datasets with
279 acoustic data identified at the 50% and 10% error risk tolerance, respectively), influential variables

280 showed consistent patterns (electronic supplementary material S13). We are therefore confident in our
281 results as they are not sensitive to the rate of error risk tolerance.

282

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

284 Landscape variables were retained in all most parsimonious models (electronic supplementary
285 material S9) and had significant effects on species-specific bat activity but no effect on CWMBSD (a
286 metric related to foraging intensity at the bat community level) and composite bat activity (electronic
287 supplementary material S13). The effect of landscape compositional heterogeneity (i.e. Shannon
288 diversity of habitats) at broad spatial scale (≥ 2 km radius scale) was always positively associated with
289 bat activity, including *E. serotinus*, *M. myotis/blythii*, *P. nathusii/kuhlii*, and *P. pipistrellus*. The
290 density of hedgerows was the most selected landscape variable in models on species-specific bat
291 activity (present in six out of nine models) but had contrasting effects: the activity of *B. barbastellus*,
292 *R. hipposideros*, and *P. pygmaeus/M. schreibersii* increased with hedgerow density while the opposite
293 was true for *M. myotis/blythii* and *Nyctalus* spp. and no significant effect was found for *Myotis* spp.
294 Additionally, the amount of coniferous forest at 4 km radius scale had a negative effect on both *B.*
295 *barbastellus* and *P. pipistrellus nathusii/kuhlii* activity whereas *R. hipposideros* was less active with
296 increasing deciduous forest cover at the small spatial scale (50 m radius scale). The density of river at
297 5 km radius scale was positively related with the activity *P. pipistrellus* and *P. pygmaeus/M.*
298 *schreibersii*. Surprisingly, grassland cover had negative effects on open-space forager activity (*E.*
299 *serotinus* and *Nyctalus* spp.).

300

301 **4. Discussion**

302 Our field experiment shows conclusively that bat activity and foraging intensity at foraging
303 habitats are affected by the presence of very high voltage power lines (VHVPL). Overall, our results
304 indicate that relative humidity mediates the effects of power lines on bats as we detected bat attraction
305 to power lines at high relative humidity levels (i.e. when corona discharges occur) and avoidance of
306 power lines by bats at low relative humidity levels (i.e. when no corona discharges are expected).

307 While the underlying mechanisms remain to be tested, the former result is consistent with
308 expectations from our hypothesis that light emitted by VHVPL due to corona discharges would attract
309 insects and therefore increase bat foraging intensity near VHVPL. From the four potential non-
310 exclusive mechanisms that could explain power line avoidance by bats, our results suggest that any
311 negative effects of VHVPL on bats are most likely due to the physical presence of the power lines
312 and/or exposure to extremely low frequency electromagnetic fields. Noise, light and high frequency
313 EMFs arising from corona discharges seemed to play no role in explaining avoidance of power lines
314 by bats.

315 We found that relative humidity exacerbated bat activity and community-level foraging
316 intensity at foraging habitats near power lines compared to control sites. Among many other factors,
317 corona discharges at power lines mainly occur during wet conditions [17] and result in the emission of
318 UV and blue light with peaks within the range of 230-440 nm [19]. The so-called ‘corona light’ has
319 shown to be responsible of power lines avoidance by reindeer [59], but given its spectrum it may
320 attract nocturnal insects [25, 26] and thus bats. Interestingly, we found attraction to power lines in
321 both light-tolerant (e.g. *P. pipistrellus*) and light-sensitive (e.g. *B. barbastellus*) bat species and no
322 attraction or avoidance in other light-sensitive bats present in our study area including species (e.g.
323 *Myotis* spp.) that may perceive UV and short wavelength blue light [60, 61]. While we did not
324 specifically test the corona effect on insect prey, previous studies have highlighted clear positive
325 relationships between insect abundance and bat (foraging) activity [62-64]. Furthermore, our results
326 not only suggest changes in bat activity but also changes in bat behaviour with increased foraging
327 intensity near power lines when corona discharges occur (i.e. at high relative humidity levels), thus
328 implying that changes in bat activity mirror bat responses to their insect prey. Direct measurements of
329 insect abundance in relation to corona discharges are however needed to confirm the process
330 involved. Indeed, other factors such as high frequency EMFs due to corona discharges could also be
331 at play (e.g. by disrupting sensory orientation of bats), but so far the only studies assessing the effects
332 of electromagnetic fields on bats have suggested either a negative effect on bat activity and foraging
333 intensity [35, 36] or no impact [37], albeit at much higher frequencies. Further research is also

334 required to identify the distance at which this cascading effect operates to fully appreciate the
335 mechanisms involved.

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

350 Our prediction on power line avoidance by high-flying and open-space foragers due to the
351 physical structure (pylons and cables) of the power lines was supported by our results on *Nyctalus*
352 spp. which showed significantly higher activity at control sites than near VHVPL regardless of the
353 weather conditions. The *Nyctalus* species group includes *N. noctula* and *N. leisleri*, two open-space
354 forager species that forage at height [70]. Our results for *Nyctalus* spp. corroborates those of
355 Kahnonitch, Lubin [14] who revealed that the activity of the open-space and high-flying forager *T.*
356 *teniotis* decreases closer to 161 KV power lines. Overhead wires greatly vary in height depending on
357 topography (from 10 m to >50 m, especially in our hilly study area) and may overlap with the flight
358 height of *Nyctalus* spp., thus potentially representing obstacles while foraging/commuting.

359 However, we also observed power line avoidance by other bat species (*B. barbastellus*, *E.*
360 *serotinus*, *P. pipistrellus*, and *P. pygmaeus/M. schreibersii*) and reduced composite activity and
361 foraging intensity at power lines, but only at low relative humidity levels. Wing morphology of these

362 bat species makes them more manoeuvrable than *Nyctalus* spp. [11] and it seems unlikely that
363 overhead wires represent physical barriers to movement for these species. As our sampling design
364 does not disentangle the effects of extremely low frequency electromagnetic fields (50 Hz) generated
365 by the VHVPL and the physical presence of VHVPL on bats, the potential negative effect of
366 electromagnetic fields on bats cannot be excluded. The mechanisms underlying the avoidance of
367 power lines by bats merits further investigation and further behavioural experiments are therefore
368 needed to assert our findings.

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

384

385 **Ethics**

386 Ethical approval was given by University of Stirling Biological and Environmental Sciences Ethical
387 Committee.

388

389 **Data accessibility**

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

394

395 **Authors' contributions**

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

399

400 **Competing interests**

401 We declare we have no competing interests.

402

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406

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- 596

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

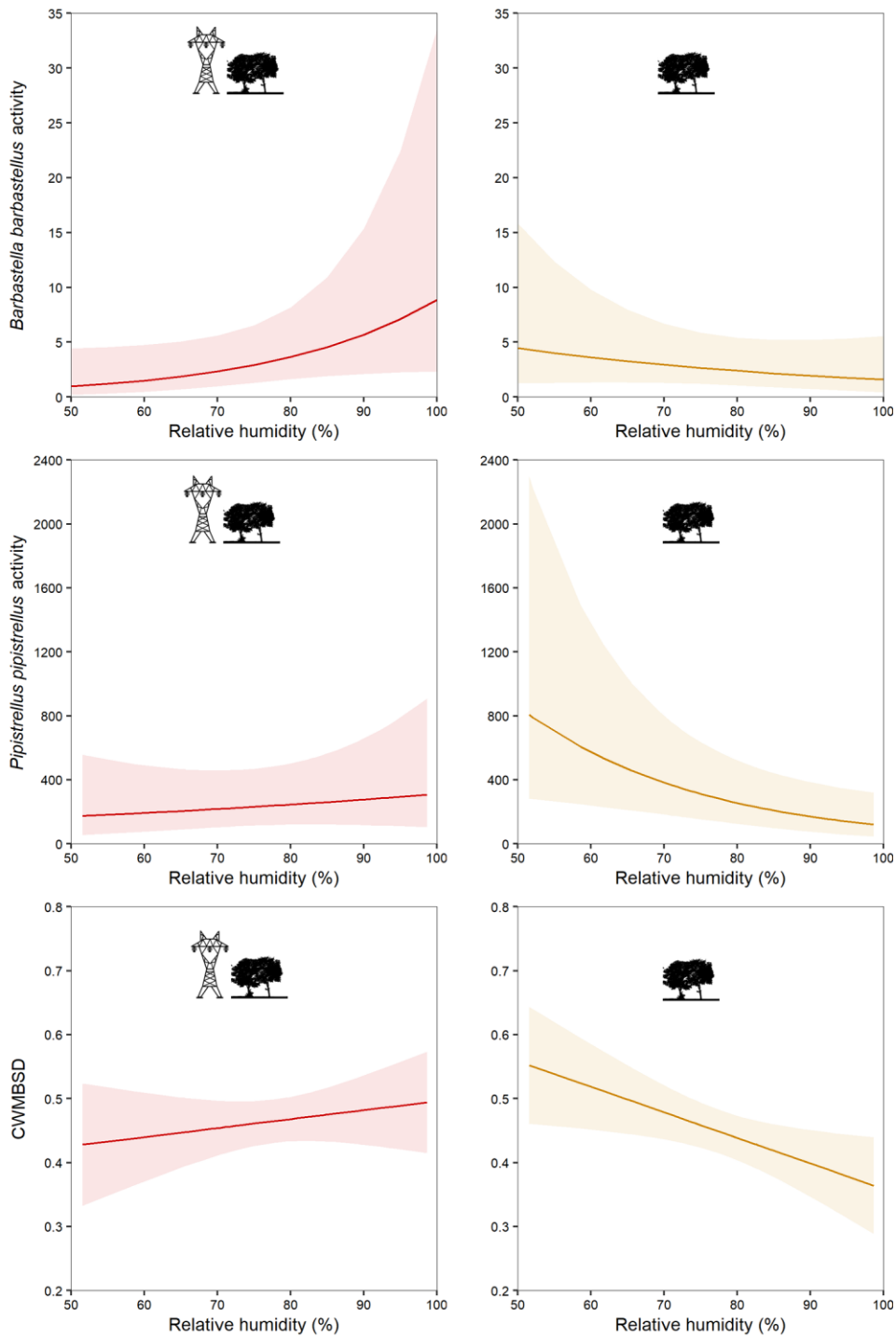
Potential effects investigated	Expected responses
Physical presence of power lines (pylons and cables)	High-flying and open-space species (-)
Electromagnetic fields	All species (-)
Corona discharges: noise	Passive-listening species (-)
Corona discharges: light	Light-tolerant species (+) Light-sensitive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

600

601 **Table 2.** Standardized, model-averaged parameter estimates with associated standards errors (SE) and 85, 95% and 98% confidence intervals (CIs) of the
602 best (G)LMMs ($\Delta AICc < 6$) relating the effects of very high voltage power lines, humidity, and their interaction on bat taxon-specific activity, composite bat
603 activity and community weighted mean bat sequence duration (CWMBSD). CIs that do not overlap zero are represented in bold red (85% CI: weak evidence;
604 95% CI: moderate evidence; 98% CI: strong evidence). Description of the most parsimonious models can be found in electronic supplementary material S10
605 and full results of the models in the electronic supplementary material S12.
606

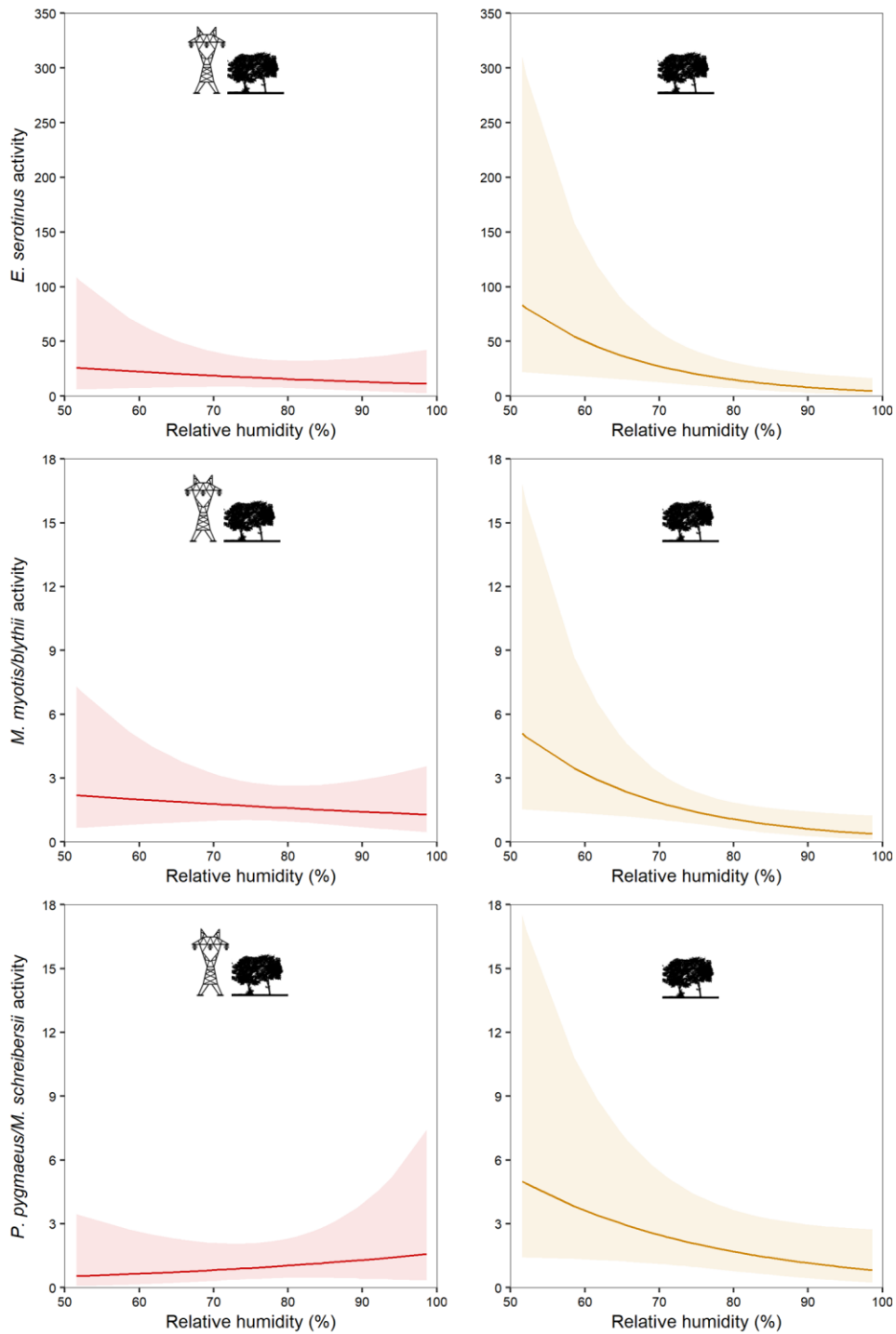
Variable		<i>Barbastella barbastellus</i>	<i>Eptesicus serotinus</i>	<i>Myotis myotis/blythii</i>	<i>Myotis</i> spp.	<i>Nyctalus</i> spp.	<i>Pipistrellus nathusii/kahlii</i>	<i>Pipistrellus pipistrellus</i>	<i>Pipistrellus pygmaeus /Miniopterus schreibersii</i>	<i>Rhinolophus hipposideros</i>	Composite 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

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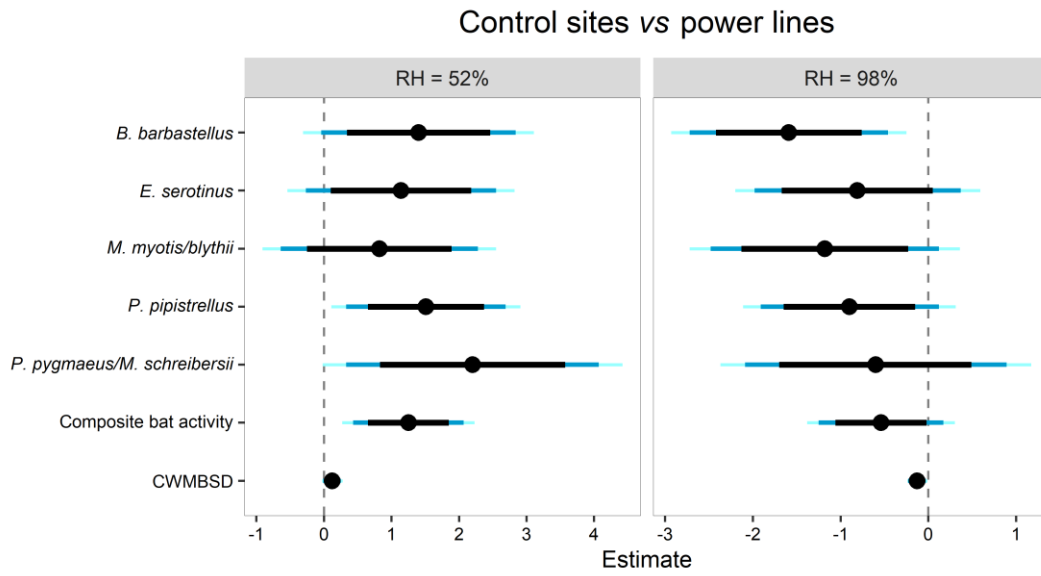
609 **Figure 1.** Predicted bat responses with the 95% confidence interval to relative humidity at forest
 610 edges along very high voltage power lines (≥ 220 kV, VHVPL) (left hand panels, red) and control sites
 611 (right hand panels, orange). Predictions were obtained from models in which the interaction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



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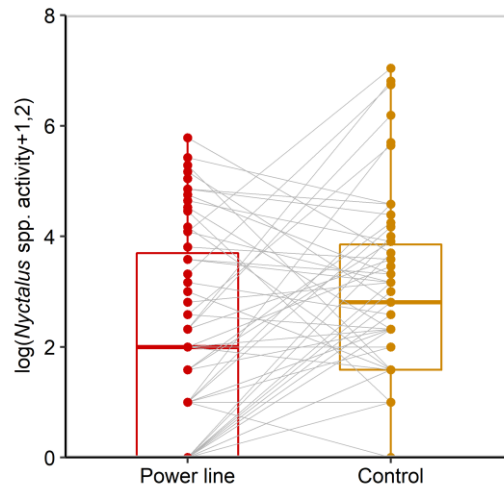
616 **Figure 2.** Predicted bat responses with the 95% confidence interval to relative humidity at forest
 617 edges along very high voltage power lines (≥ 220 kV, VHVPL) (left hand panels, red) and control sites
 618 (right hand panels, orange). Predictions were obtained from models in which the interaction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

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624 **Figure 3.** Pairwise comparisons of bat activity and foraging intensity (CWMBSD) between control
 625 sites and power lines at each extreme value of the relative humidity gradient sampled (i.e. 52 and
 626 98%). Estimates and associated 85%, 95% and 98% confidence intervals of the comparisons are
 627 represented with black points and black, dark-blue and light-blue bars, respectively. Positive estimates
 628 indicate higher bat activity and increased foraging intensity at control sites compared to power lines.



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630 **Figure 4.** Boxplot of *Nyctalus* spp. activity (number of bat passes per night on a logarithm scale to the
 631 base 2) recorded at forest edges along very high voltage power lines (≥ 220 kV) and control sites. Dots
 632 represent raw data with paired sites and nights linked with a grey line. The boxplots display the
 633 interquartile range box (top line = 75% of the data \leq this value; middle line = median; lower line =
 634 25% of the data \leq this value) and the lower and upper whiskers (minimum and maximum data points).

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