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Modelling landscape connectivity for greater horseshoe bat using an empirical quantification of resistance

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Abstract

1. Habitat fragmentation and isolation as a result of human activities have been recognized as great threats to population viability. Evaluating landscape connectivity in order to identify and protect linkages has therefore become a key challenge in applied ecology and conservation.

2. One useful approach to evaluate connectivity is least-cost path (LCP) analysis. However, several studies have highlighted importance of parameterization with empirical, biologically relevant proxies of factors affecting movements as well as the need to validate the LCP model with an independent dataset.

3. We used LCP analysis incorporating quantitative, empirical data about behaviour of the greater horseshoe bat *Rhinolophus ferrumequinum* to build up a model of functional connectivity in relation to landscape connecting features. We then validated the accumulated costs surface from the LCP model with two independent datasets; one at an individual level with radiotracking data and one at a population level with acoustic data.

4. When defining resistance, we found that the probability of bat presence in a hedgerow is higher when the distance between hedgerows is below 38 m, and decrease rapidly when gaps are larger than 50 m. The LCP model was validated by both datasets: the independent acoustic data showed that the probability of bat presence was significantly higher in areas with lower accumulated costs, and the radiotracking data showed that foraging was more likely in areas where accumulated costs were significantly lower.

5. *Synthesis and applications.* Through our modelling approach, we recommend a maximum of 38 m (and no more than 50 m) between connecting features around colonies of greater horseshoe bats. Our quantitative study highlights the value of this framework for conservation: results are directly applicable in the field and the framework can be applied to other species sensitive to habitat loss, including other bats. Provided that it is parameterized with empirical, biologically relevant

data, this modelling approach can be used for restoring and evaluating green networks in agri-environmental schemes and management plans.

KEYWORDS
acoustic monitoring, bats, corridor, fragmentation, gap-crossing, landscape connectivity, least-cost modelling, *Rhinolophus ferrumequinum*

1 | INTRODUCTION

Habitat fragmentation induced by human activities has been recognized as a great threat for population viability (Kareiva, 1987; Quinn & Harrison, 1988), leading to immediate and time-delayed biodiversity loss (Krauss et al., 2010) and biotic homogenization (Clavel, Julliard, & Devictor, 2011). In order to mitigate these impacts, growing attention is being paid to connectivity between patches of habitats (Crooks & Sanjayan, 2006; Fahrig et al., 2011) relying on the creation or protection of habitat linkages; i.e. land that promotes movement or dispersal of plants or animals between core habitats (Briers, 2002). Connection between habitats facilitates dispersal (Haas, 1995), gene flow (Manel, Schwartz, Luikart, & Taberlet, 2003; Mech & Hallett, 2001) and ultimately reduce the extinction risks of species (Brown & Kodric-Brown, 1977). Connectivity is now a key aspect in applied ecology and environmental policies. For example, the EU 2020 Biodiversity Strategy requires that by 2020 ecosystems and their services are maintained and enhanced by establishing green infrastructure connecting the network of natural and seminatural protected areas.

To achieve this goal, one needs to define linkages between core habitats at the relevant (landscape) scale (Crooks & Sanjayan, 2006). This connectivity is usually assessed with landscape modelling. However, while a consensus exists regarding the role of connectivity as essential to the persistence of fragmented populations, researchers often disagree when choosing the methodology for designing linkages for conservation (Rayfield, Fortin, & Fall, 2011; Rothley & Rae, 2005). Among available methods, the least-cost path (LCP) analysis is probably the most widely used modelling approach (LaRue & Nielsen, 2008; Phillips, Williams, Midgley, & Archer, 2008; Sawyer, Epps, & Brashares, 2011). LCP analysis provides potential paths based on minimizing the cumulative cost of movements between two points where the resistance values to movement are quantified in the landscape matrix (Chardon, Adriaensen, & Matthysen, 2003), at least on an arbitrary scale (Beier, Majka, & Spencer, 2008). Resistance estimates are thus critical in providing biologically relevant LCP models (Beier et al., 2008; Sawyer et al., 2011; Zeller, McGarigal, & Whiteley, 2012). From an applied point of view, quantifying relevant links between movements and habitats and then transforming them into landscape resistance is a key aspect to provide connectivity models useful to conservation (Keeley, Beier, & Gagnon, 2016) and, at the same time, to avoid misleading and costly recommendations (Chetkiewicz, St. Clair, & Boyce, 2006). Various approaches have been used to parameterize these resistance surfaces, but they are mainly based on experts' opinions and/

or meta-analysis assessing the importance of landscape elements in facilitating the movement of individuals (Beier et al., 2008; Spear, Balkenhol, Fortin, McRae, & Scribner, 2010; Zeller et al., 2012).

In a review, Sawyer et al. (2011) pointed out three main weaknesses in connectivity studies that used LCP analysis. First, few studies assess whether (generally coarse-grain) habitat maps are suitable proxies for factors affecting animal movement with an explicit, empirical justification. In fact, modellers often use expert opinion to assign resistance values to remotely sensed landscape traits, rather than quantifying resistance as it might be perceived by the species (the so-called "functional connectivity", Kindlmann & Burel, 2008; Taylor, Fahrig, & With, 2006). They do so mainly because empirical data are sparse or nonexistent for most species (Fagan & Calabrese, 2006). Furthermore, models based on behavioural processes are expected to be more accurate and efficient to design and implement landscape linkages (Chetkiewicz et al., 2006). Among these, Resource Selection Functions (RSF, i.e. any quantitative model that yields values proportional to the probability of use of a resource unit, Boyce, Vernier, Nielsen, & Schmiegelow, 2002) calculates the probability of use of landscape variables and represents an efficient method to quantify resistance to movements (Zeller et al., 2012), on condition that the animal's behavioural state is correctly estimated (Abrahms et al., 2017). Secondly, few studies validated their model with independent, empirical data to assess the robustness of the projection in the landscape. When performed, empirical validations sometimes show poor prediction performance of modelling. For example, LaPoint, Gallery, Wikelski, and Kays (2013) observed poor prediction performance of their corridor models build with GPS-tracked fisher data when they confronted them with independent data from camera traps. Thirdly, many studies lack justification when translating LCP model outputs into optimal corridor placement of various lengths and widths, as a problem of transferability could occur. In fact, habitat linkages could be designed at a coarse-grain scale (at which the remote-sensing environmental datasets were available), but the analysis missed important biological aspects at finer scales, at which the animal perceives its habitats and the movement process operates. For example, high-quality microhabitats can be selected by animals in areas that appear unsuitable at a macro-level (Mortelliti & Boitani, 2008). In a recent review focusing on the use of RSF in connectivity modelling, Abrahms et al. (2017) made the same conclusion, observing that most studies should suffer from misleading estimates of landscape resistance and models often lack validation with independent data.

Here we used the RSF framework and quantitative, empirical behavioural data of the greater horseshoe bat, *Rhinolophus*

ferrumequinum (Schreber, 1774), to build up a LCP model of functional connectivity in relation to landscape corridor use. We then validated this model with two independent datasets, one at an individual level with radiotracking data and one at a population level with acoustic data. Landscape resistance was estimated from the probability of crossing a gap in a connecting feature as a function of this gap width (see Awade & Metzger, 2008; Hale, Fairbrass, Matthews, Davies, & Sadler, 2015; Lechner, Doerr, Harris, Doerr, & Lefroy, 2015 for a general framework) when greater horseshoe bats commute from roost to foraging areas. We focused on this short-range echolocating species (maximum range of 10 m, Barataud, 2015) because the greater horseshoe bat is known to be strongly dependant on connecting landscape features like hedgerows for foraging and commuting (Dietz, Pir, & Hillen, 2013; Duvergé & Jones, 1994; Froidevaux, Boughey, Barlow, & Jones, 2017). Furthermore, bat populations play an important role on ecosystems and appear to have suffered a large world-wide decline (see review in Jones, Jacobs, Kunz, Willig, & Racey, 2009), which is why all bat species are protected in Europe by the Annex IV of the Habitat Directive (92/433/EEC). Although the greater horseshoe bat is widely distributed in Europe and considered as least concern (LC) on the IUCN Red List, it is listed in Annex II of the Habitat Directive which implies specific designation of protected areas because of several factors that led to a drastic decline in western populations during the last century, including agricultural intensification, roost destruction and habitat changes (Hutson, Mickleburgh, & Racey, 2001). Species that are very sensitive to connectivity loss, like bats, retain more and more attention in landscape ecology studies in relation to corridor features like hedgerows (Fonderflick, Azam, Brochier, Cosson, & Quékenborn, 2015; Heim, Treitler, Tschapka, Knörnschild, & Jung, 2015; Kelm, Lenski, Kelm, Toelch, & Dziock, 2014). Furthermore, using biologically relevant connectivity models based on species sensitive to connectivity loss should offer a great opportunity to provide a general framework for designing or testing effective green networks in this context.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

Permission for bat capture and telemetry was granted by the association *Nature Environnement 17*, France, and delivered by the French Ministry of Sustainable Development and Ecology. The study was approved by the administration of the *Direction Régionale de l'Environnement, de l'Aménagement et du Logement*.

2.2 | General information about the study area and the greater horseshoe bat's nursery colony

The study (*c.* 200 km^2) took place in Western France, 8 km around the greater horseshoe bat's nursery colony of the village of Annepont (45°50′N; 0°37′W). This lowland landscape is mainly covered by intensive agriculture (34%, mainly cereals, rapeseed and sunflower), deciduous forest (36%), grasslands (11%), villages (6%) and vineyards (9%). Hedgerows are mainly concentrated in valleys and around villages (density >20 m/ha) and scarce in intensive agriculture areas (density <5 m/ha). In the study area, population density is 52.6 inhabitants per km^2, mainly located in small villages or isolated farms where artificial lighting at night is scarce or absent. The effect of artificial lighting on connectivity (Azam, Le Viol, Julien, Bas, & Kerbiriou, 2016; Hale et al., 2015) was thus not taken into account in this study.

The nursery colony of *c.* 100 greater horseshoe bat females (in association with *c.* 275 females Geoffroy's bats, *Myotis emarginatus*, E. Geoffroy, 1806) was discovered in 2013 in the roof of the city hall, and has been studied since this discovery with weekly counts at emergence during spring and summer. No other large horseshoe bat colony was found within 20 km despite intensive research with ultrasonic recorders and capture sessions. All field samplings (acoustic and radiotracking) were performed at the same period between 11 and 22 July 2016 when the majority of females were lactating. In fact, as energetic constraints for reproductive females change during the breeding season (and also resource availability in space), one should expect variability in foraging behaviour throughout this period (e.g. Flanders & Jones, 2009; Goiti, Aihartza, Garin, & Zabala, 2003). In order to ensure minimal behavioural variability over time associated to changes in energetic demands and to ensure correct interpretation of the variance observed in the data, we conducted the study over a short time period (12 days). Time is expressed at local time (GMT + 2 hr). For the study period, civil sunset occurred at *c.* 22.25 hr, civil sunrise at *c.* 05.45 hr. At this period, according to weekly counts, greater horseshoe bats first leave the colony primarily between 22.05 and 22.30 hr.

2.3 | Empirical assessment of landscape resistance using gap-crossing method

As discontinuities in corridors can act as barriers to animal movements, gap-crossing probabilities can be used to quantify empirical landscape resistance (Awade & Metzger, 2008; Hale et al., 2015). The probability of crossing a gap in a given hedgerow was estimated as a function of the width of the gap when greater horseshoe bats commute from roost to foraging grounds at the start of the night (22.00–22.55 hr local time, see Supporting Information Figure A1 in Appendix S1). We placed recorders (full-spectrum bat detector Song Meter SM3BAT, Wildlife Acoustics Inc. USA) in hedgerows with various gap widths (one gap per hedgerow, n = 38, from 10 to 130 m) within 1.5 km from the colony for one night (for more details see Supporting Information Appendix S2). To avoid bias in crossing events detection in small gaps (a bat approaching but not crossing could be detected behind gaps as small as 5 m), the model was set with gaps larger than 10 m. This distance corresponds to the maximum detection distance for this species (Barataud, 2015). Microphones were positioned horizontally at 1.5 m high in hedgerows just behind the gap furthest away from the colony. They were

orientated to the colony (see Supporting Information Figure A2 in Appendix S1) as greater horseshoe bats emit ultrasound waves in a very narrow beam from the front of the head (Schnitzler & Grinnell, 1977). For these two reasons, if a greater horseshoe bat was detected during the commuting period at the beginning of the night, we assumed that it crossed that specific gap. Gaps and microphone placements were carefully chosen to ensure that greater horseshoe bat detection could be clearly associated to only one gap. Ultrasound recordings were analysed with the toolbox *Tadarida* (Bas, Bas, & Julien, 2017), which identifies species-specific echolocation calls. This software automatically detects and extracts sound feature parameters of the recorded echolocation calls and classifies them into known classes according to a probability value that a call is from a specific group or bat species using a random forest algorithm (Cutler et al., 2007). All calls checked by listening the sequence with a ×10 time expansion and inspecting spectrograms. As the other European *Rhinolophidae*, greater horseshoe bat, presents very specific echolocation calls with nearly constant frequency (79–83 kHz, Barataud, 2015), the resulting classification probabilities were very high.

Only presence/absence acoustic observations between 22.00 and 22.55 hr local time were considered, corresponding to the commuting period to foraging grounds (see Supporting Information Appendix S1). The probability of crossing a gap in a connecting feature during commuting (i.e. overall presence/absence of a bat behind a gap during this period, $n = 38$ gaps) was estimated with logistic modelling (GLM with a binomial error distribution, link=logit), with the width gap with its quadratic term and the distance to the colony as explanatory variables.

2.4 | Connectivity modelling

In order to model the landscape connectivity, a LCP approach was used with the R package *gdistance* (Van Etten, 2017). For calculation advantages in this package, conductance rather than resistance (conductance = permeability = 1/resistance) was used for transition matrix, so we used this term rather than resistance in the rest of the study. Following the gap-crossing approach (Hale et al., 2015), we hypothesized that the conductance was directly related to the distance to connecting features that facilitate bat movements (hedgerows, woodlands, vineyards and suburban areas like villages and farms, Duvergé & Jones, 1994, 2003; Fonderflick et al., 2015), with a maximum value of conductance when the bat is in the connecting feature and a decreasing conductance as the bat flies away the feature.

2.4.1 | Environmental datasets

All the major connecting features that could be used by greater horseshoe bat during commuting between colony and foraging areas (hedgerows, woodlands, vineyards and suburban areas like villages and farms, Duvergé & Jones, 1994, 2003; Fonderflick et al., 2015) were digitalized within the 8 km radius circle centred on the colony, using QGIS 2.8.9 (QGIS Development Team, 2015)

and high-resolution aerial orthophotographs (taken in 2014 with 20 cm resolution, Institut National de l'Information Géographique et Forestière, France). In addition, field validations were performed during the field session in July 2016. The resulting vector layer of connecting features was rasterized (at 8 m × 8 m cell resolution) and minimum Euclidean distance to the nearest feature was calculated with the R package *raster* (Hijmans & van Etten, 2016).

2.4.2 | Conductance matrix and connectivity modelling

The conductance matrix was estimated by applying the previous logistic model (probability of gap-crossing as a function of distance) on the raster of distance to the nearest connecting feature. As a result, a raster was obtained with a resolution of 8 × 8 m, representing the predicted probabilities of greater horseshoe bat presence according to distance to connecting features. Then these predicted probabilities were standardized (max = 1, min = 0) and values in connecting features were set at 10 to facilitate movements in connecting features (analogue to classical resistance values ranging from 1 to 100, see Sawyer et al., 2011). As large roads like highways could represent an important barrier for bats (Berthinussen & Altringham, 2012), cell values for highways (larger than 30 m) were set to 0, except at bridges or tunnels. Two highways (E5 and E602) of 30 m width are present in the study area. This conductance raster was used to calculate the between-cells transition matrix, with cells connected with their eight orthogonal and diagonal nearest neighbours. A correction by distance between cell centres ("geocorrection") was done by dividing each conductance matrix value by the distance between cell centres. Finally, the accumulated cost surface was estimated for each cell of the landscape using the colony as the origin location. The LCP between two cells on the raster and the associated distance were obtained with Dijkstra's algorithm (Dijkstra, 1959).

2.5 | Validation of connectivity model by independent and empirical data

During the same period, we carried out two additional surveys (acoustics and radiotracking) with the aim to provide an independent dataset for assessing the performance of our landscape connectivity modelling.

2.5.1 | Validation by acoustic approach

To validate the connectivity model, ultrasonic recorders were placed in 75 favourable habitats (hedgerows and woodlands, Dietz et al., 2013; Flanders & Jones, 2009) for one night at a maximum distance of 8 km from the colony (maximum distance according to our radiotracking work), with microphone directed horizontally at a 90° angle from a hedgerow (if relevant), at 1 m height (see Supporting Information Appendix S2 for details). This validation dataset was distinct from the previous one that was used for estimating the gap-crossing probability model. For validation, recorders were not

placed in unfavourable habitats like open fields to be sure to relate absence of bats as a function of connectivity and not to habitat suitability. With the aim to assess the performance of our connectivity model, we hypothesize that the probability of presence of greater horseshoe bat in favourable habitats during the commuting period should be better explained by the accumulated cost from the colony than other variables like distance to colony. To test this, distance and accumulated cost values from the colony were calculated for these acoustic locations and included in logistic models (GLM with a binomial error distribution, link=logit) explaining overall presence/absence of commuting greater horseshoe bats at an acoustic location during the commuting period ($n = 75$).

2.5.2 | Validation by radiotracking approach

Localizations of radio tagged greater horseshoe bats from the Annepont colony were investigated during their nocturnal movements. Eight lactating females were radio tagged with LB-2X radiotransmitters (Holohil Systems Ltd, Canada). Sessions of radiotracking were carried out on these individuals using the "homing in" approach (White & Garrott, 1990), which involved following the bats as closely as possible (without disturbance) to localize them when they forage (see Supporting Information Appendix S2 for more details).

To assess the performance of the connectivity model, we hypothesize that the probability of presence of foraging radio tagged bats should be higher in more connected areas, i.e. where accumulated costs are lower, taking into account distance to colony and habitats. To assess if radiotracking locations during foraging were randomly situated according to accumulated cost surface calculated from the connectivity model, we compared accumulated costs at random locations (five random fixes for one foraging fix, at the same distance and in favourable foraging habitats: forests and hedgerows) and those at observed radiotracking fixes during foraging (one individual location every 30 min to ensure temporal independence, see Supporting Information Appendix S2 for more details). This comparison used the standardized difference calculated as follows:

$$StdzdDiff = (AccCost_{random} - AccCost_{foraging})/AccCost_{foraging}$$

$AccCost_{random}$ is the accumulated cost from the model at the random location and $AccCost_{foraging}$ is the accumulated cost from the model at the foraging location. This difference was then tested against the value 0 (i.e. expected value under the null hypothesis if greater horseshoe bats foraged randomly according to the $AccCost$ model output) using a mixed model (GLMM with a Gaussian error distribution) with individual ID as random term on intercept. The 95% confidence interval of this difference (i.e. the intercept term) was estimated using a parametric bootstrap with 500 simulations (Bates, Mächler, Bolker, & Walker, 2015).

2.6 | Statistical analysis

All the analyses were done with R 3.3.2 (R Development Core Team, 2016). Statistical models were validated by a visual inspection of

the residuals to satisfy their conditions of application. Model selection procedure was based on the Akaike information criterion with a correction for finite sample sizes and considering best models with $\Delta AIC_c > 2$ (Burnham & Anderson, 1998). In the case of models with equivalent AIC_c or when $\Delta AIC_c < 2$, the principle of parsimony was applied, keeping the model with the lower number of parameters. Mixed models were computed with the *lme4* package (version 1.1-12, Bates et al., 2015).

3 | RESULTS

### 3.1 | Empirical assessment of landscape resistance using gap-crossing method

The presence of greater horseshoe bats in gaps was assessed using acoustic sampling (Figure 1) around the colony, the gap width in a corridor was significantly the best predictor explaining the probability of crossing during the commuting period (Table 1; slope = −0.036, intercept = 1.368). The probability of crossing decreases from 0.80 for gaps smaller than 10 m to less than 0.05 for gaps larger than 130 m (Figure 2). According to this model, the value of gap width where the probability drops below 0.50 was of 38 m, and half of the maximum probability ($p = 0.40$) was reached with a gap of 49 m.

3.2 | Connectivity modelling

The gap-crossing logistic model was applied on a raster representing the distance to connecting features (hedgerows, woodland, village and vineyard) calculated for the whole study area (i.e. 8 km from the colony). The resulting raster can be viewed as representing the probability of presence of a greater horseshoe bat during commuting related to landscape features that facilitate movements. This raster was used as a permeability map for calculating accumulated cost from the colony using a LCP approach (Figure 3).

3.3 | Validation of the connectivity model

With the aim to assess the performance of our connectivity model, we first mobilized an independent acoustic dataset. During the commuting period in the beginning of the night, greater horseshoe bats were detected in 27 out of 75 sampling sites (36%). Model selection based on AIC showed that presence/absence of greater horseshoe bats was best explained by the model "Accumulated Cost" (Table 2). This model (Figure 4) showed the lowest AIC_c value and a higher value of the coefficient of discrimination, Tjur's R^2, as a standard measure of explanatory power for logistic GLM (Tjur, 2009). The other models (*Distance to Colony* and the constant [null] model) showed less explanatory power. When considering acoustic observations for the whole night instead of during the commuting period only, presence/absence of greater horseshoe bats was significantly explained by the model *Distance to Colony* rather than *Accumulated Cost* (for details see Supporting Information Table A in Appendix S3).
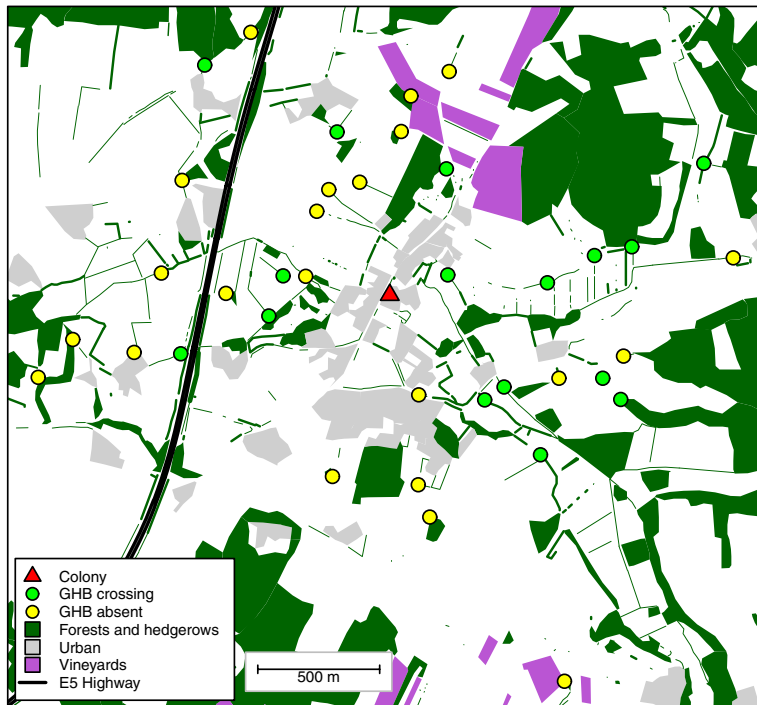
FIGURE 1 Acoustic sampling locations (circles, *n* = 38) for testing the effect of gap width in connecting features. Greater horseshoe bat absence/presence refers to sampling for one night during commuting time (early night: 30 min before and 25 min after the sunset). White background refers to open space

A second assessment of our connectivity model performance was done at the individual level, using data provided by the radio-tracking session. Location data were obtained for eight reproductive females (average of 7.13 independent foraging fixes per individual, average distance of 4.22 km from the colony, maximum of 7.58 km, see Supporting Information Table B in Appendix S4 for details). The comparison between the accumulated cost values at random locations and those at foraging locations observed during the radiotracking session indicates that the difference was significantly greater than 0 (Table 3), meaning that radiotracking locations of foraging greater horseshoe bats were situated in areas where accumulated costs from the colony were significantly lower than random locations at comparable distances to colony and in favourable habitats.

4 | DISCUSSION

In this study, we used a framework combining a RSF (to provide a quantitative estimate of the landscape resistance) with a LCP analysis, to propose a connectivity model which was then validated with two independent datasets. Using the gap-crossing method, we retrieved a quantitative, empirical dataset of greater horseshoe bat behaviour to estimate a biologically relevant estimation of landscape connectivity.

We focused on reproducing (lactating) females as they are a key to explaining population dynamics and conservation. The energetic constraints for reproductive females vary during the breeding season, in addition to availability of resources, therefore variations in foraging behaviour are expected through this period (e.g. Flanders & Jones, 2009; Goiti et al., 2003). This could be also expected for the gap-crossing behaviour, so, before extrapolating

this model, one needs to validate our findings for other periods or other classes of individuals (males, juveniles, nonreproductive or pregnant females). We could also expect that the parameters of the gap-crossing model should be different in landscapes with different connectivity characteristics. We hypothesize that crossing a gap is a trade-off between cost (exposure to predation in this case) and benefit (use of a shorter path for access to a foraging area instead of longer path without gap). Across the species range, we may expect that parameters of the gap-crossing model could be different in landscapes with different connectivity characteristics. Compared to other regions where the greater horseshoe bat is present, our study area shows moderate hedgerow densities (35 m/ha, data from the French Institute of Forestry 2007, see http://www.polebocage.fr/-Bocage-and-hedgerows-in-France,136-.html). In the UK, for instance, densities of hedgerows around greater horseshoe bat colonies range between 20 and 65 m/ha (Froidevaux et al., 2017). In landscapes with a higher density of hedgerows, we should expect a steeper slope for the model (more negative slope value), as large gaps should be rare and less used (there are more alternatives available for large gaps). In landscapes with lower hedgerow densities, a less negative value should be expected for the slope of the model, as bats should more frequently use larger gaps to reach their foraging grounds (less alternatives for large gaps). It would be interesting to test this and conduct gap-crossing studies in different landscape contexts across the species distribution to ensure replicability. The proposed design allows testing this in different landscape configurations, and also for various species sensible to connectivity loss. Moreover, the estimated value of the slope could be a general parameter characterizing sensitivity to connectivity, useful when comparing different landscapes or species.

TABLE 1 Results of model selection for explaining gap-crossing probability of commuting greater horseshoe bat as a function of distance to the colony and gap width in connecting feature (*n* = 38)

Models	K	AIC_c	ΔAIC_c	AIC_c weight	Cum. weight	Log likelihood
~Gap width	2	46.60	0.00	0.57	0.57	−21.13
~Dist.Colony + Gap width	3	48.91	2.31	0.18	0.75	−21.10
~Gap width² + Gap width	3	48.94	2.34	0.18	0.92	−21.12
~Gap width² + Gap width + Dist. Colony	4	51.41	4.81	0.05	0.98	−21.10
~1	1	53.84	7.24	0.02	0.99	−25.86
~Dist. Colony	2	55.00	8.40	0.01	1.00	−25.33

Note. Models are ranked from best (top) to worst according to AIC_c. *Gap width* is the width in connecting feature (m). *Dist. colony* is the distance to the colony, Superscript "2" indicates a quadratic effect.
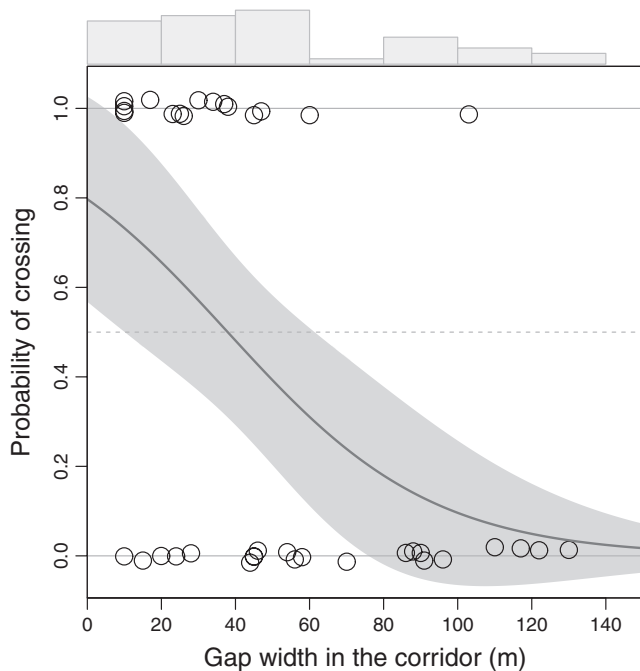

FIGURE 2 Probability of crossing a gap in a connecting feature as a function of its width during commuting period for greater horseshoe bat. Observations (*n* = 38 gaps, dots) are jittered to increase visibility. Top histogram in grey refers to the gap width distribution. The large, black line indicates the predicted probability from the selected binomial GLM model and the grey area indicates its 95% confidence interval

Reviews of Sawyer et al. (2011) and Abrahms et al. (2017) pointed out the need for connectivity modelling with empirical input based on underlying behavioural processes when defining resistance matrix and also the need for validating models with independent data. Estimating landscape resistance based on movement preferences at finer scales is expected to be more relevant to land management (Chetkiewicz et al., 2006). Here we defined landscape resistance at fine scale (grain size of 8 m), estimating empirically the probability of presence during movement period as a function of the distance to landscape features favourable for movements. Our LCP model was then validated with two independent datasets: one with radiotracked greater horseshoe bats that

were more found in areas where accumulated costs of moving were significantly lower; the other using acoustic sampling showing that probability of presence of greater horseshoe bats during the beginning of the night (commuting time to reach foraging grounds) was significantly higher in areas with lower accumulated costs. Interestingly, when considering acoustic data for the whole night, the probability of presence of greater horseshoe bats was significantly better explained by the distance to the colony rather than the accumulated cost, confirming the importance of defining the conductance based on relevant underlying behavioural processes (Abrahms et al., 2017), in this case when the bats commute at the start of their night-time forage.

Despite a growing and valuable interest for connectivity in bat conservation, to our knowledge all but one (Hale et al., 2015) of the studies focusing on connectivity modelling (for bat species) estimated a landscape resistance based on expert insight or from Species Distribution Modelling outputs (Henry, Pons, & Cosson, 2007; Le Roux et al., 2017; Razgour, 2015; Roscioni et al., 2014; Tournant, Afonso, Roué, Giraudoux, & Foltête, 2013). The "gap-crossing" framework adopted in our study could be largely used for other species or sites to obtain an empirical measure of parameters affecting movement resistance. This is particularly true for short-range echolocating species like greater horseshoe bats (maximum echolocating range: 10 m) that are rarely detected with passive acoustic recorders (Barataud, 2015). By placing acoustic recorders (or other methods, see below) with various linkage configurations to be tested (in the case of this study, several distances between hedgerows) in the vicinity of a focal point (here a breeding colony), one can define RSF as the probability of moving in these connecting features as a function of their characteristics and use these for defining resistance matrix in connectivity modelling. Importantly, attention has to be paid to correctly translating these estimates to biologically relevant resistance. Firstly, detected presence should be related to an animal leaving the focal location (i.e. known departure location). Detection of other individuals coming from other locations should have different constraints in their movements and this may introduce some noise to the data or bias when calculating the accumulated cost. In our study, the closest known greater horseshoe bat colony is as far as 20 km away, so greater
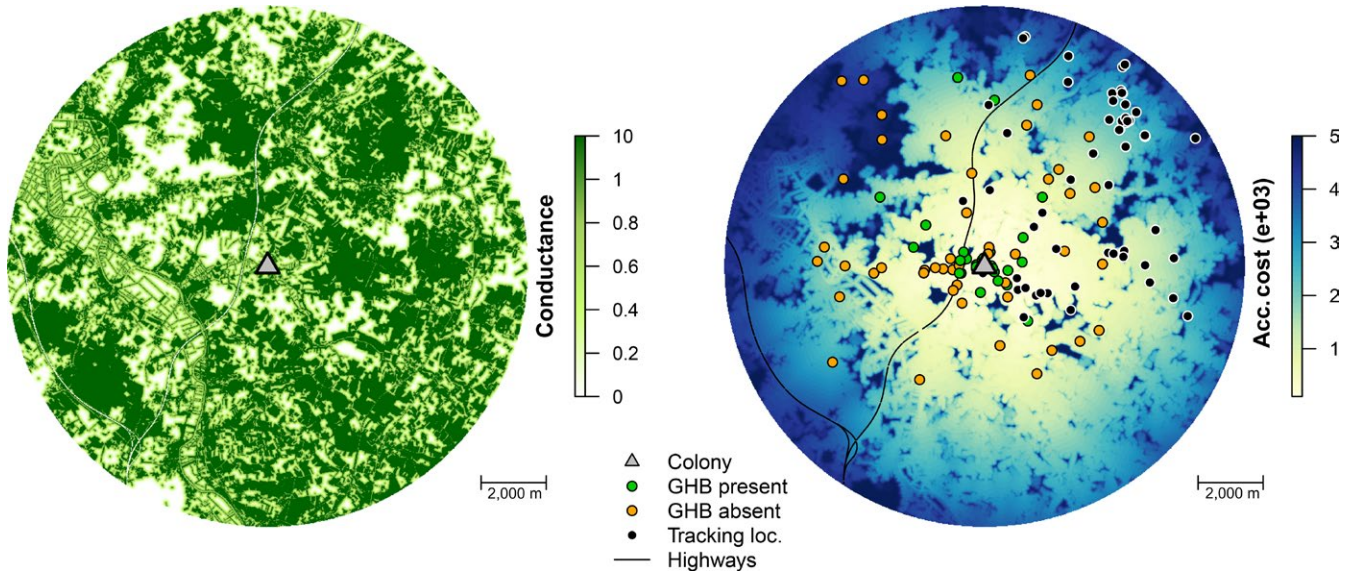
FIGURE 3 Conductance (left) and accumulated cost surface (right, colour scale according to quantiles) estimated from the colony, as predicted from the "distance to features" model. The green/yellow dots show the locations of acoustic sampling used for validation. The black dots show the locations of eight radiotracked greater horseshoe bat females also used for validation

TABLE 2 Results of model selection in order to validate the accumulated cost surface models, explaining the presence of greater horseshoe bat during the commuting period ($n = 75$ locations, for one night each) as a function of distance and accumulated cost from the colony. The last column shows the coefficient of discrimination, Tjur's R^2, as a standard measure of explanatory power for the two models

Models	K	AIC_c	ΔAIC_c	AIC_c weight	Cum. weight	Log likelihood	Tjur's R^2
~Acc.Cost	2	82.85	0	0.59	0.59	−39.34	0.241
~Dist. Colony	2	83.57	0.72	0.41	1.00	−39.70	0.236
~1	1	100.07	17.21	0.00	1.00	−49.01	—

horseshoe bat detections within a 1.5 km radius could be reasonably attributed to an individual leaving and commuting from the Annepont colony. Secondly, detection should be done according to the appropriate behavioural state (see Abrahms et al., 2017), here when greater horseshoe bats commute from the colony to foraging grounds through connecting features at the beginning of the night. As hedgerows or other features could also be used for foraging by greater horseshoe bats later during the night, we only considered observations before 22.55 hr. As expected, when assessing the performance of the connectivity model, acoustic observations for the whole night (instead of data restricted to the commuting period) did not validate this model as the probability of presence was better explained by the distance to colony and not by accumulated cost. One possible explanation for this could be that bats are better channelled in the beginning of the night when commuting in relation to landscape features than later when they disperse to various habitats searching for prey. Lastly, to correctly convert fine scale behaviour characteristics defined by RSF to the estimation of resistance at the landscape scale, one needs to map the habitat features as relevant proxies at the relevant grain size according to the actual perception of the species (Sawyer et al., 2011). In our case, all potential connecting features (hedgerows and tree lines,
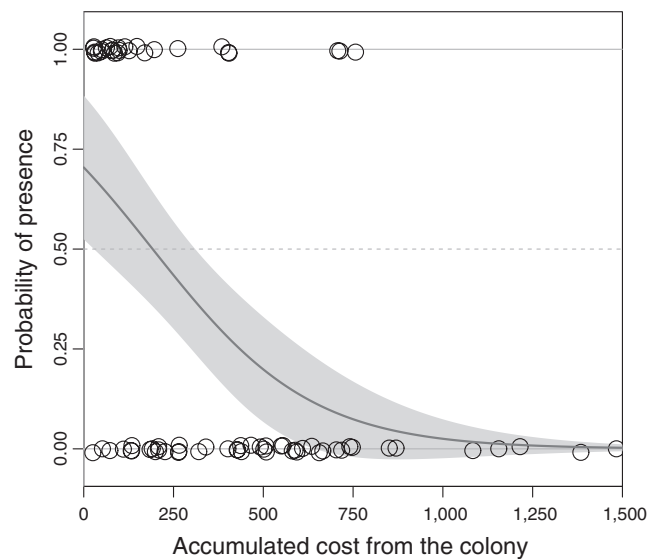
FIGURE 4 Probability of presence of a greater horseshoe bat (during commuting time) as a function of accumulated cost from the colony at sampling locations used for acoustic validation ($n = 75$). Observations (dots) are jittered to increase visibility. The large black line indicates the predicted probability from the selected binomial GLM model and the grey area is its 95% confidence interval

TABLE 3 Estimates of standardized differences between accumulated costs at random locations and accumulated costs at the tracking locations from the modelling scenario. These standardized differences were estimated with mixed models *StdzdDiff* ~1 with individual ID as random effect. The 95% confidence intervals were estimated with a parametric bootstrap

Parameter	Estimate	SE	t-value	2.5% CI	97.5% CI
StdzdDiff	0.0596	0.0264	2.254	0.0048	0.1099

forests, villages and vineyards) were digitalized and the distance to features were calculated on 8 m resolution raster, below the effect of the distance to features determined by RSF (38–50 m). By taking into account these recommendations, we think that this framework can be successfully applied to many other species to estimate landscape resistance and to identify corridors.

Hedgerows are known to be important for movements of several taxonomic groups (for examples see review of Davies & Pullin, 2007). Several early studies of various bat species showed that hedgerows are frequently used as foraging grounds, and also as commuting routes between roosts and feeding sites (e.g. Entwistle, Racey, & Speakman, 1996; Limpens & Kapteyn, 1991; Verboom & Huitema, 1997), including the greater horseshoe bat (i.e. Duvergé & Jones, 1994). Our study validates the important role of natural and seminatural elements like hedgerows, treelines and forests as connecting features for greater horseshoe bats. Using radiotracking in the Grand Duchy of Luxembourg, greater horseshoe bats were observed commuting along hedgerows from their roosts to their foraging grounds (Dietz et al., 2013). At a larger scale, a recent study found that greater horseshoe bat colony size in UK was positively related to density of linear features (Froidevaux et al., 2017). Using acoustic sampling, Frey-Ehrenbold, Bontadina, Arlettaz, and Obrist (2013) also showed the importance of connectivity in farmland

landscapes for bats, with shorter-range echolocating bats being particularly sensitive to habitat fragmentation, despite them not detecting any horseshoe bats in their study. In our study, we quantified the role of landscape features acting as corridors by estimating the distance between hedgerows that allows a realized connectivity for greater horseshoe bats. According to Figure 2, the probability of presence in the connecting features is high when the distance between hedgerows is lower than 38 m, and then decreases rapidly with gaps larger than 50 m with a maximum of 130 m. It may be surprising that a greater horseshoe bat can cross an open area larger than its echolocation range (maximum 10 m), but bats have important navigation abilities at several scales (from home-range up to continent when migrating), and spatial memory is believed to play an important role in navigating in a familiar environment (see review in Holland, 2007), for example by the use of landmarks (Jensen, Moss, & Surlykke, 2005). For these reasons, we expect that the distances to landscape features should be different when moving in unknown environments where the bat has to find its route with a limited perceptual range (e.g. during juvenile dispersal).

4.1 | Application for conservation

We suggest that the approach used here, combining a RSF definition with the gap-crossing method and a LCP modelling, is applicable to many other species sensitive to connectivity loss, and could provide quantitative information that can be directly applied to conservation. Our study shows that this framework is biologically relevant, as the connectivity model is validated at both individual and population levels. In this framework, a key component is the estimation of gap-crossing probabilities measured in the field, as this information is then turned into relevant resistance in the connectivity model. These gap-crossing probabilities

FIGURE 5 Relative connecting values for natural connecting features (hedgerows and woodlands) in the vicinity of the colony of Annepont (France) and for the whole study area (inset), as an illustrative example of application for conservation of the accumulated cost model

could be estimated using various techniques to provide reliable estimates for resistance of surfaces according to the target species: visual observations (e.g. Lees & Peres, 2009), playback trials (e.g. Bélisle & Desrochers, 2002), audible or ultrasonic acoustic recorders (this study), camera traps and PIT transponders (Soanes, Vesk, & van der Ree, 2015), etc. Furthermore, this probability of crossing could be directly applied in the field to orientate conservation (e.g. where to plant trees to effectively ensure connectivity). In the case of this study, we found that a distance of 38 m (maximum of 50 m) between landscape features ensures an effective connection for greater horseshoe bats in their resident environment.

As connectivity loss is recognized as a threat for many species (including bats), some authors recommend practical thresholds for linear habitat management in order to ensure effective connectivity. For example, Entwistle et al. (2001) recommends filling gaps in hedgerows as small as 10 m to benefit bats, but without explaining how this distance was defined. Such a threshold approach is relatively common in recommendations and also in gap-crossing or connectivity studies (e.g. Lechner et al., 2015). Behavioural relationships with connecting features are better described as a gradient along a continuum (framework of RSFs) and could be more effectively incorporated in connectivity modelling using probability of use. They can then be usefully applied in conservation scenarios to promote effective movements between core habitats (Chetkiewicz & Boyce, 2009). As a further application for conservation, the model output provides quantitative spatial predictions that can be used as an efficient mapping tool for landscape planners and conservationists. One can calculate and map the relative connecting values for corridors (here hedgerows and woodlands, see Figure 5 and Supporting Information Appendix S5 for calculation details), in order to identify the need for protecting high connecting elements and for enhancing or restoring low connecting ones. The framework presented here for estimating resistance can be used on many other species, to assess their sensitivity in connectivity loss, and ultimately provide relevant insights to be integrated in connectivity modelling and corridor planning. Such models are also able to provide quantitative predictions to be tested as a tool (see Supporting Information Appendix S6 for an example) for evaluating green infrastructure policies.

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AUTHORS' CONTRIBUTIONS

D.P., F.C., C.K. and M.L. conceived the ideas and designed methodology; D.P., F.C. and M.L. collected the data; D.P. and F.C. analysed the data; D.P. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Acoustic data are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.g1t3680 (Pinaud, Claireau, Leuchtmann, & Kerbiriou, 2018a).

Raw acoustic data are also archived and available via the French citizen science programme "VigieChiro" http://vigienature.mnhn.fr/page/participer-vigie-chiro, at the portal http://vigiechiro.herokuapp.com/ with the following site ID: 170692, 170732, 170733, 170734, 170735, 170774, 170776, 170777, 170817, 170818, 170858, 170859 and 170861.

Tracking data are available via Movebank https://doi.org/10.5441/001/1.3pk82706 (Pinaud, Claireau, Leuchtmann, & Kerbiriou, 2018b).

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SUPPORTING INFORMATION

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