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Finding a method to predict the commuting activity of bats

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Résumé

Alors que de nombreuses espèces de chauves-souris sont considérées comme menacées en Europe, les corridors de vol utilisés par les chauves-souris entre leur gîte et leurs territoires de chasse restent peu connus. La prise en compte des éléments permettant la connexion entre les habitats étant l'un des buts principaux des mesures de conservation, nous avons voulu trouver un modèle de prédiction pour les déplacements journaliers des chauves-souris à l'échelle du paysage. Deux espèces avec des adaptations différentes pour la navigation ont été étudiées, une fortement liée aux structures verticales (*R. hipposideros*) et une plus adaptée aux vols en espaces ouverts (*M. myotis*). Des données acoustiques ont été récoltées à 30 emplacements autour de six gîtes pour chaque espèce, incluant des situations „structurées“ (à proximité de structures verticales, considérées comme de potentielles balises acoustiques) et des situations plus ouvertes. Nous avons modélisé la relation entre l'activité enregistrée et un grand nombre de variables environnementales. La sélection des variables les plus importantes a été effectuée à l'aide du Least Absolute Shrinkage and Selection Operator (LASSO). Nous avons trouvé le modèle prédictif optimal en utilisant la validation croisée, en utilisant des données indépendantes pour tester la qualité de prédiction. L'activité des deux espèces était liée à des paramètres tridimensionnels des structures verticales, ce qui indique que la modélisation de l'habitat des chauves-souris devrait prendre en compte l'arrangement spatial à échelle fine. Les espaces ouverts, l'éclairage nocturne ainsi que les routes et les bâtiments ont également été sélectionnés comme prédicteurs. La prédiction de l'activité de vol donne un nouvel aperçu des patterns de déplacement des chauves-souris à l'échelle de paysage, et propose des différences interspécifiques. Les modèles de prédiction sélectionnés sont d'un intérêt particulier pour la conservation des chauves-souris, et pourraient être utilisés à large échelle, n'impliquant qu'un investissement informatique mineur.

Abstract

Whereas bat species are still widely endangered across Europe, the commuting corridors that many species use between their roost and the surrounding foraging areas remain poorly known. Since including connective elements is important for conservation plans, we aimed to find models for predicting the commuting activity of bats in an agricultural landscape. We focused on two species of bats with different adaptations for navigation, one with a strong relationship to vertical structures (*R. hipposideros*), and one adapted to more open-space situations (*M. myotis*). We sampled acoustic recordings around six roosts for each species, at 30 sampling locations, surveying situations with vertical structures (assumed to be attractive acoustic landmarks) and in more open spaces. We modelled the relation between the activity recorded at the locations and a large number of environmental predictors. Automatic model selection using Least Absolute Shrinkage and Selection Operator (LASSO) was performed to select the most relevant predictors. We found the best predictive model for each species by cross-validation, using training and testing sets to evaluate the prediction performance. The activity of both species was related with three-dimensional arrangement of landscape features, supporting that bat habitat should be modelled considering fine scale spatial parameters. Predictors reporting open spaces as well as artificial light and distance to structures were also selected. Predictions on a map provided new insight in the understanding of bat movements at the commuting scale, showing species-specific patterns of landscape use. The prediction models that were found have a valuable interest for bat conservation, and could be widely used while only involving limited computational investment.

Keywords: landscape connectivity, spatial representation, echolocation, model selection, LASSO, habitat modelling

Introduction

Within vast rural areas of Europe, human pressure is reducing the heterogeneity of the landscapes, leading to a loss of habitat that affects species at multiple scales (Stoate et al., 2001; Piessens et al., 2005; Hendrickx et al., 2007; Gámez-Virués et al., 2015). Bat populations have shown a strong decline due to the modification of their habitats, observed in the second half of the 20th century (Voigt and Kingston, 2015), and conservation measures are only enabling a slow recovering of targeted species (Van der Meij et al., 2014). The main threats for European bats are habitat loss due to intensification of agriculture and changes in silvicultural practices, urbanization and habitat fragmentation caused by the development of roads and lighting systems, and the likely reduction of prey availability (for a synthesis, see Voigt and Kingston, 2015). Many species are living in the vicinity of humans, being directly affected by changes in practices in multiple ways. The high sensitivity of bat populations to perturbations is mainly linked with their high ecological requirements (use of several different and precise habitats) and their low reproduction rate. The concern for bats decline has risen in the past decades, leading to an international cooperation through the European agreement for bats conservation (UNEP/Eurobats).

The protection of habitat for bats being a main goal in conservation strategies (Hutson et al; 2015), this habitat has to be clearly described for each species. Bat habitat can be separated in three categories: the “roost”, the “foraging area”, and, if they are spatially explicit, their connective elements referred as “commuting corridors”. Daytime roosts are well known for species roosting in human settlements, which mostly allows their legal and practical protection. The protection of hunting habitats is less targeted and predominantly covered by

other nature conservation measures (forest edges, wetlands, etc.). However, our knowledge concerning commuting corridors is mostly lacking, leaving practitioners with only little concrete information to efficiently protect this complex and networked habitat. Commuting corridors are the flyways used by bats use between the roost and the foraging area. No reliable and complete description of this habitat exists, although the topic is discussed since a long time (Limpens and Kapteyn, 1991; Verboom, 1998). Homogenisation and fragmentation due to the intensification of human activities occurring in European rural areas (Jaeger et al., 2011) leads to loss of connectivity, isolating habitat patches for bats as it is for other species (Debinski and Holt, 2000). Even if the functionality of connective habitats, generally referred as “ecological corridors” in conservation biology, is a target in the European strategy for habitat conservation (Tillmann, 2005), the effectiveness of ecological networks as conservation tool is debated (Beier and Noss, 1998; Horskins, 2005; Boitani et al., 2007; Gilbert-Norton et al., 2010) and relies on a realistic description of this complex and often specie-dependant habitat (Boitani et al., 2007).

Obviously, the domain of bats conservation is facing this problem, since the connective elements within bat habitat are only little known. From a conservation view, formulating a predictive model to represent ecological processes, such as species current or future distributions, is one of the most relevant contributions that scientific research can bring to practice. A prediction can serve as an operational tool, as practitioners can directly use it as a basis for prioritization in habitat or species conservation plans. This tool can be especially useful when the habitat is not well defined by prior knowledge, i.e. when knowledge about the underlying factors explaining the species distribution in a landscape is limited. In the case of bat commuting corridors, such a tool might be very useful, considering the poor definition of this habitat. Until now, no modelling technique has been attempted on bats commuting corridors. For comparison, relatively complex, multi-scale models have been implemented to

predict habitat suitability for bat distribution (Bellamy et al., 2013) and bat roosts (Bellamy and Altringham, 2015).

On their flyways, bats navigate and evaluate their environment through echolocation, by comparing ultrasounds that they emit with the echo returned by the background structures. Hence, these background structures are used as landmarks for navigation at small scale (Barchi et al., 2013; Jensen et al., 2005; Moss and Surlykke, 2010), and on the commuting routes (Limpens and Kapteyn, 1991; Verboom, 1998). Daily commuting between the roost and the foraging areas certainly requires a combination of spatial memory at landscape scale and the use of acoustic landmarks to define the position at both small scale (position in space) and corridor scale (localization on the corridor) (Barchi et al., 2013; Jensen et al., 2005; Schnitzler et al., 2003). A series of acoustic landmarks is assumed to define a guideline in the landscape that will be followed more or less strictly by the commuting bats.

In the literature, only few studies were explicitly interested in acoustic landmarks used by bats on commuting routes. These previous insights only considered rather simple landscape characteristics, for instance the presence of vertical structures (e.g. hedgerows) or linear elements (e.g. streams) (Limpens and Kapteyn, 1991; Verboom, 1998; Verboom et al., 1999). Hence, more complex landscape parameters that would more realistically represent bat soundscape have not been explored yet. However, previous insights in bat echolocation world support that bat soundscape is more complex than previously considered in studies focused on commuting activity. For instance, it was demonstrated that parameters such as structural heterogeneity (Jung et al., 2012) or three-dimensional settings of vertical structures (Froidevaux et al., 2016) are strongly related to species composition in forest. These studies suggest that bat habitat should be modelled at fine, three-dimensional scale, since spatial characteristics are related to adaptations for foraging and navigating in specific habitats. The relationship with more complex spatial parameters is now easily explored, thanks to the

evolution of high-resolution methods for spatial representation such as LiDAR. Species-specific adaptations for navigation such as echolocation frequency and wing morphology suggest that commuting routes are species-specific (Schnitzler and Kalko, 2001; Stilz and Schnitzler, 2012). For instance, species with a long echolocation range are more likely to fly through open spaces than species with restricted echolocation range, which are relying on close acoustic landmarks. Hence, different bat species can be assumed to be more or less dependant on landmarks, or to use different type of landmarks. Finally, landscape composition at larger scale might affect commuting bats. For example, it was shown that the lighting system (Hale et al., 2015; Stone et al., 2009) and the development of road network (Bennett and Zurcher, 2013; Berthinussen and Altringham, 2012; Kerth and Melber, 2009; Russell et al., 2009) have a negative impact on landscape connectivity for bats.

We aimed to develop a method for predicting the activity of commuting bats in the landscape. For this purpose, we collected activity data of two bat species along potential commuting corridors, and used a set of landscape variables to find the models that would allow the most accurate prediction of this activity. We propose that these models might be used as a basis to predict the commuting corridors of bats in the landscape, and result in a new tool for land-use management. These models might also be valid for other species with similar ecology as the ones studied here.

Material and methods

Study design, data collection and statistical analyses were aimed to propose models for the prediction of the commuting activity of two bat species with different ecological requirements. We used landscape features that potentially affect the connectivity, either acting as guidelines or as barriers for bats, as predictors. In order to allow some comparisons between the two species, the same procedure was followed. This study was conducted in the Swiss Central Plateau and close pre-alpine areas (Fig. 1).

Selection & description of study species

Among the 30 bat species present in Switzerland, only the ones fulfilling the following criteria were considered: a) Commuting species (spatially explicit roost & foraging area) b) Distribution range and foraging habitats well known c) Local knowledge (local experts & monitoring of the roost) is available. Corridors are expected to be species-specific, because species' echolocation resolution and range are highly specialized among species (Stilz and Schnitzler, 2012; Moss and Schnitzler, 1995). Hence, species adapted to fly in open space situations will certainly commute differently than species, which are more closely bound to landmarks due to a shorter detection range. In order to extend the validity of the study, we chose two species with different flight adaptations: the Lesser Horseshoe Bat (*Rhinolophus hipposideros*) and the Great Mouse-eared Bat (*Myotis myotis*). The models for each species might be possibly used as models for other species with similar ecology.

Rhinolophus hipposideros uses human infrastructures as summer roost, and forages mainly in forest. For this species, distance between these two habitats is usually less than 1 km (Bontadina et al., 2002; Mitschunas and Wagner, 2015; Reiter et al., 2013). There is strong evidence that the Lesser Horseshoe Bat uses vertical elements such as hedgerows as guidelines to commute between the roost and the foraging area (Motte and Libois, 2002; Zahn

et al., 2008), and that they are negatively affected by light when commuting (Stone et al., 2009). This species is very adapted to spatially structured environment (e.g. vegetation) considering wing morphology and echolocation (calls at high and constant frequency), with short detection range and very fine representation of the structures and especially movements (insect flutter detection) at small distance. Populations showed a significant decline in the 1950's-1960's in central and western Europe, due to a general decrease of habitat quality and contamination by pesticides (Bontadina et al., 2002, 2000). *R. hipposideros* is monitored in Switzerland since 2000 (Bontadina et al., 2006).

Myotis myotis also roosts in human settlements, and mostly hunts in open deciduous forests, orchards, and above freshly cut meadows (Arlettaz, 1996; Audet et al., 1990; Drescher, 2004). It commutes in average 6 to 9km (but until 25km) to its foraging area (Arlettaz, 1996). Its commuting behaviour is not well known and difficult to observe as it is a relatively fast and mostly low flying species, and the use of specific landscape features as navigation landmarks has never been demonstrated. Considering the characteristics of its echolocation signal, this species seems adapted to detect background structure at relatively long distance (Boonman and Schnitzler, 2005), and thus to fly in more open spaces without problems navigating. Since that the commuting behaviour of species adapted to navigate in more open habitats, such as *M. myotis*, is usually poorly known, we were interested to see if the method would also be suitable for predicting their commuting activity, and suggest the existence of landmark-elements on which they rely for commuting. E.g., elements such as roads or railways might act as barriers, as it was already demonstrated for other species of the *Myotis* genus (Kerth and Melber, 2009; Vandeveldel et al., 2014). This specie declined in the 1970's-1980's due a significant loss of summer roosts, a consequence of building renovation and contamination by wood treatment products (Bohnenstengel et al., 2014). Monitoring is established in Switzerland since 1990.

For both species in the majority of roost the populations are slowly recovering in recent years, as rigid conservation measures take effect (Bohnenstengel et al., 2014).

Study period

Each study site was sampled four times, during two different periods of activity, with an interval of min. 7 days between passages in a given period. Only adults were flying during activity period 1 (recordings from 19th May to 8th July), whereas juveniles that were born during the summer were also flying during activity period 2 (recordings from 24th July to 1st September). Each activity period was sampled two times, with an interval of minimum seven days between each passage (Table 1). The exact dates of birth and first flights vary between sites and years, and were provided by local surveyors for each site. We hypothesized that juveniles would need a training period to learn to navigate, thereby changing perceived overall spatial activity pattern from a “commuting activity” pattern during the period of activity 1, to a “commuting and learning” pattern during the period of activity 2. The aim was to assess if the spatial activity pattern changed when the juveniles were flying.

Nights with unfavourable conditions (rain, strong wind or temperature <7°C) and full moon (+/- 1 night) were avoided. Bat activity was recorded from 15 minutes before sunset to 15 minutes after sunrise.

Selection of study sites

The distribution range of *M. myotis* widely spreads over the Central Plateau, and in low altitude valleys of the Alps and Jura mountains. *R. hipposideros* is restricted to a few low altitude valleys of the Alps and the Jura mountains.

As commuting corridors connect the roost and the foraging areas, a *study site* was defined as a delimited area with the roost in the centre. Six study sites were selected for each of the two species, in order to account for variance in habitat composition that occurs between different geographical areas. The criteria to select the study sites were: a) roost and foraging area are not directly connected (bats have to commute on at least 40 meters between both) b) annual count of the roost colony size is implemented since several years c) most recent count showed at least 25 individuals and the roost colony is not subject to important inter-annual fluctuations according to annual monitoring. Among the sites that met the selection criteria, we selected the six sites with the largest colonies as study sites (Fig. 1). Due to the rarity of *R. hipposideros*, four of the six study sites were distributed within an area of ~ 10x2.5km. However, considering the distances separating the roosts (at least 2.5km) and the short movement scale of this species, as well as the abundance of hunting territories at short distance from these roosts, we considered that activity recorded at these sites was independent from each other. Roosts were always in a building of a settlement, sized between 500 to 5'000 inhabitants for *R. hipposideros*, and 1'000 to 16'000 for *M. myotis*. Around settlements, landscape was rural, composed by a mix of agricultural and forested patches, with regional differences in landscape composition.

The extent of the *study sites* was fixed at ~400 meters around the roosts. This radius was chosen considering that a) *study sites* had to be wide enough to represent the different habitats bats are flying through while commuting, i.e. including rural environment outside of the settlement, b) ratio of sampling effort versus expected data yield would increase with the sum square of the distance to the roost (decreasing probability of encountering a bat “by chance” the further from the roost), and c) that sampling effort was directly limited by the available equipment.

Table 1. summary of Study Sites and passages. Colony size corresponds to the number of adults in the roost in June or July 2016

Species	Site	ID	Colony size	Period 1		Period 2	
				Passage 1	Passage 2	Passage 3	Passage 4
<i>R. hipposideros</i>	Metzerlen	1	41	09/06/2016	07/07/2016	18/08/2016	29/08/2016
	Amsoldingen	2	64	21/06/2016	03/07/2016	19/08/2016	30/08/2016
	Kleinteil	3	400	15/06/2016	04/07/2016	23/08/2016	01/09/2016
	Giswil	4	38	22/06/2016	05/07/2016	22/08/2016	31/08/2016
	Sarnen	5	16	06/06/2016	28/06/2016	17/08/2016	25/08/2016
	Sachselsn	6	83	26/05/2016	23/06/2016	15/08/2016	24/08/2016
<i>M. myotis</i>	Eysins	7	500	17/06/2016	30/06/2016	29/07/2016	05/08/2016
	Courtételle	8	446	08/06/2016	06/07/2016	25/07/2016	01/08/2016
	Burgdorf	9	300	14/06/2016	29/06/2016	28/07/2016	03/08/2016
	Beggingen	10	488	07/06/2016	08/07/2016	24/07/2016	02/08/2016
	Steinen	11	140	20/05/2016	26/06/2016	26/07/2016	06/08/2016
	Altendorf	12	94	19/05/2016	27/06/2016	27/07/2016	07/08/2016

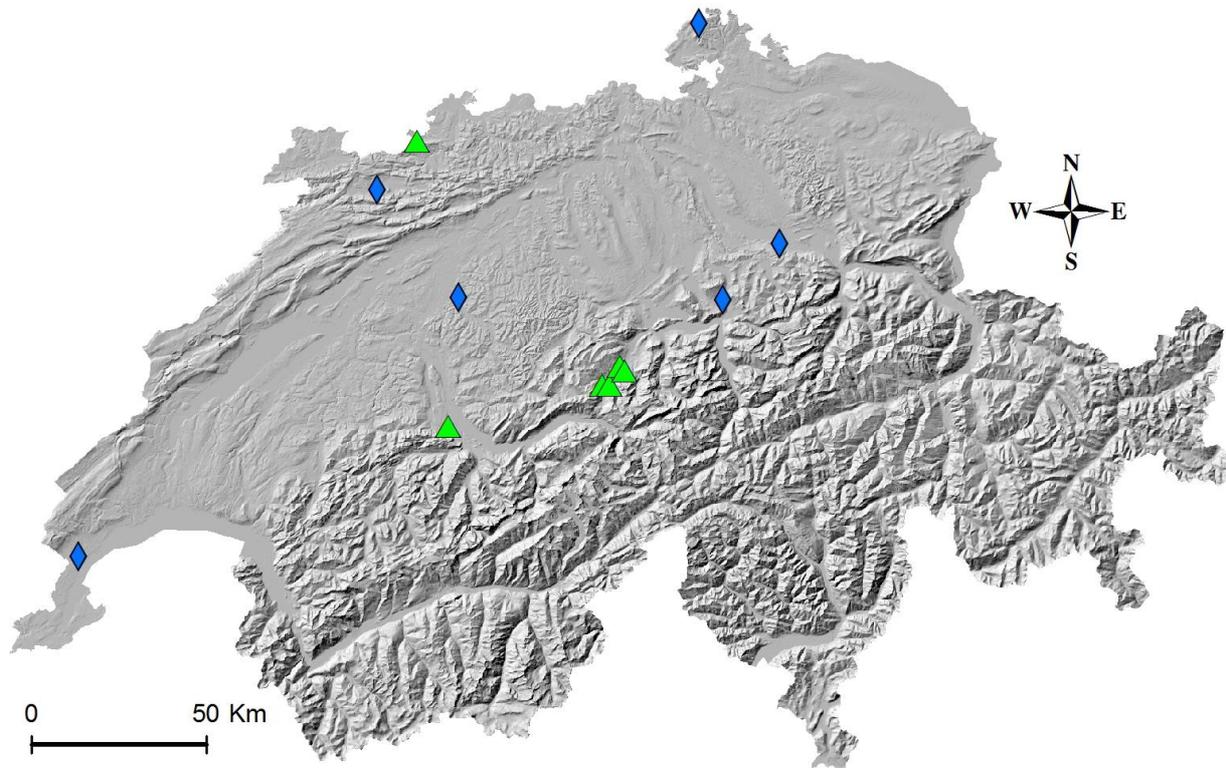


Fig. 1. Localization of the 12 study sites. Green triangles: *R. hipposideros* sites; Blue diamonds: *M. myotis* sites

Data collection and spatial setting

Sampling locations were defined as the places where commuting activity of bats was acoustically measured within the study sites. The level of bat activity can be derived from recordings of echolocation calls. We used automatic ultrasound recorders (BATLOGGER, Elekon AG, Lucerne, Switzerland) to record bats. The devices are equipped with an ultrasound microphone, sensitive within +/- 5 dB between 10 and 150 kHz. The omnidirectional microphones were fixed on a plastic stick ~1.5 meters above ground, pointing slightly towards the ground to protect from direct rain. Automatic recording was triggered by ultrasound signals by setting the recording mode to “Period” and fixing a pre-trigger of 500 ms and a post-trigger of 1’000 ms. Sampled at 312.5 kHz, the recordings were then stored in wav-files of maximally 10 sec duration, which we termed a “sequence” (a small succession of ultrasound signals recorded).

We defined 30 sampling locations (referred to as “Locations 1 to 30”) around the roost at each study site. Locations were distributed on three circles around the roost – with either 60, 190 or 350 meters radius from the roost. 6 locations were chosen on the inner (60 meters radius) circle, 9 on the mid (190 meters radius) circle and 15 on the outer (350 meters radius) circle, resulting in average gap sizes (i.e. mean distance between 2 adjacent locations of the same circle) of 60, 130 and 145 meters, respectively. See Fig. 2 for an example of spatial setting at one site.

At each site, bat activity was recorded in the vicinity of vertical structure (“structured” locations, 2/3 of locations), and in more open environments (“open” locations, 1/3 of locations). At “structured locations”, the microphone was placed close to a vertical structure, defined as an element >1.5m above-ground (generally vegetation or buildings), at a distance of ~2m for *M. myotis* and <1.5m for *R. hipposideros*, oriented parallel to the structure edge to record bat passages along the structure. We included different types of vertical elements (e.g.

isolated trees, hedgerows, buildings, walls, etc). At “open locations”, the recorder was set as far as possible from any structure, to include situations where bats are crossing open spaces. The estimated detection range of the two species served as reference to define a minimum distance to structure from the microphone, in order to be in a true “gap” situation from the bat’s point of view. However, such a minimum distance is difficult to estimate, since the bat sonar is a dynamic system that adapts to the situation during navigation (e.g. distance to the target, type of surface) and the maximal detection range for a given species depends on several physiological and environmental parameters (Boonman and Schnitzler, 2005; Stilz and Schnitzler, 2012). *R. hipposideros* emits at a very high frequency, suggesting a very short detection range as high frequencies are more strongly affected by atmospheric attenuation with distance (Lawrence and Simmons, 1982). Based on personal experience, we estimated absolute maximum detection distance for *R. hipposideros* at 5m (similar values can be found in the literature; see Stilz and Schnitzler, 2012). *M. myotis* emits more distinct modulated calls at lower frequencies (Boonman and Schnitzler, 2005) and thus should be able to detect extended background structures at longer distances. We estimated the maximum detection range for *M. myotis* at 25m. Hence, it was sometimes difficult to find “true” gap situations (i.e. without vertical structure in the detection range) within settlements for this species. Locations were pre-selected using 1:5’000 aerial photography and LiDAR maps displaying structures with information about height (vertical accuracy of 1m). During pre-selection, we accounted for the different variants of “structured” and “open” situations. The final location was chosen in the field, to follow the study design described above as closely as possible. We expected higher bat activity near structured locations than near open locations, since vertical structures were assumed to be attractive acoustic landmarks for bats. Proximity to hard surfaces (less than ~1.5m from concrete ground or wall) was avoided if possible as it compromises the quality of the acoustic signals through hard echoes.



Fig. 2. Example of spatial setting of the sampling locations (red dots) at one study site, on the 60m (inner) circle, 190m (mid) circle and 350m (outer) circle. The roost is designated with the star.

Analyses of the recordings

The acoustic sequences collected on the field were automatically identified with BatScope (Boesch and Obrist, 2013), a software developed at the Swiss Federal Institute for Forest, Landscape and Snow Research WSL. This tool cuts sequences into single calls and attributes a species to each, based on three types of statistical classifiers using the characteristics of the call (or call features), based on a reference library. After automatic classification, we manually verified the sequences using successive quality filters. We used a different protocol for each species, since differentiating *M. myotis* calls from close species of the *Myotis* genus requires following supplementary refining steps. Protocols of call selection for both species can be found in Table S1. We assumed that each sequence was the recording of an individual bat flying by (vs. foraging around the microphone), taking that as a single activity record.

Selection of the environmental predictors

First, all the landscape features linked in previous studies with commuting bats were considered as pre-existing knowledge and included in the list of candidate environmental predictors. Vertical structures and linear elements such as watercourses and hedgerows have been shown as landmarks, and artificial lighting and roads as potential obstacles.

Environmental predictors are summarized in Table 2. Additionally, recent studies also suggested that the three-dimensional arrangement of the vegetation might help bats for navigation, e.g. canopy ruggedness (Froidevaux et al., 2016) or hedge and canopy structure (Jung et al., 2012). These findings support that modelling bat soundscape should be considered at a more detailed level, e.g. by reporting 3-dimensional, small-scale composition of vertical structures. Hence, we also included measure of ruggedness and height of vertical structure features. This information is increasingly available with the development of geodatabases such as LiDAR ones. Finally, we also considered variables at terrain level, as variations in topographic properties (e.g. terrain ruggedness) may also be detected and used as navigational signals by bats. Values were extracted from data sources that are now widely available. Environmental predictors were classified in five feature classes: vertical structures, structure characteristics, linear features, terrain, climate and artificial light. As lighting values are known to influence bat's flight behaviour, but were not available at large scale, we measured artificial light in the field and include it in the analyses in order to highlight a possible effect on the study species.

Measurement of the environmental predictors

Two main classes of measurements allow assessing the relation between species and landscape predictors: distance-based measurements and landscape composition-based measurements (either at a single- or at multiple-scales). The first one is the distance from a sampling location to the closest feature of an environmental predictor, and the second one

reports the abundance of a feature within a given area. As they provide different information, we combined these approaches, and let the automatic model selection (discussed later) choose the most relevant variables. Distance measurement was the Euclidian distance to the closest feature. Landscape composition metrics reported the density of the landscape feature, as well as edge-density for polygon features. Landscape composition measurements were done in circular buffers around sampling locations, at three different scales. The scales were based on the estimated maximum detection range of the sonar of the two species (respectively 5 and 25m), and an intermediate value (10 m). For ruggedness, we used three different methods of calculation (Terrain Ruggedness Index, Vector Ruggedness Measure and Curvature) that provide different information, and included all of them as variables. Description of the measurements is given in Table 3.

Two different data sources representing 3-dimensionnal characteristics of landscape features were available: one using spectral data, and the other one using LiDAR data. Considering that the quality of both varies depending on region (regarding the precision of the measurement and the year of measurement), each variable reporting 3-dimensionnal characteristics (ruggedness and height) was calculated two times: one time using the Spectral data, and one time using LiDAR data. We expected the model selection procedure to pick up the most relevant variable between both.

Variables were calculated at a resolution of 1m in Arcmap GIS 10.3.1 (ESRI 2015). Artificial light was measured at each location 2m above ground using a Voltcraft MS-1300 Digital Luxmeter (measure range from 0.1 to 50'000 lx and resolution of 0.1 lx).

Tab. 2. description of environmental predictors and measurements. Additional information about the data sources can be found in Tab. S2.

Class	Environmental predictor	Definition	Measurement	Source (see Supplementary materials)
Vertical structures	Buildings	Any type of building	Distance, Cover, Edge	swissTLM ^{3D} v 1.4
	Forest	Dense forested area	Distance, Cover, Edge	swissTLM ^{3D} v 1.4
	Isolated tree	Isolated trees with height >5m	Distance, Density	swissTLM ^{3D} v 1.4
	Tree groups	Cultivated trees (orchards)	Distance, Cover, Edge	swissTLM ^{3D} v 1.4
	Vegetation	Vegetation with height >3m	Distance, Cover, Edge	VHM
	Structures	Vertical elements (incl. vegetation) with height>3m	Distance, Cover, Edge	SHM
Structure characteristics	Structure height	Height of any structure with height >3m	Mean	nDSM-ADS; nDSM-LiDAR
	Canopy height	Height of canopy of vegetation with height >3m	Mean	VHM
	Building height	Height of any type of building with height>3 meters	Mean	nDSM-ADS minus VHM-ADS
	Canopy ruggedness	Ruggedness of canopy surface of vegetation with height >3m: calculated with 3 different methods: Terrain Ruggedness, Vector Ruggedness Measure, Curvature	Mean	DTM-LiDAR
	Structure ruggedness	Ruggedness of structure surface with height >3m: calculated with 3 different methods: Terrain Ruggedness Index (Riley et al., 1999), Vector Ruggedness Measure (Sappington et al., 2007), Curvature ¹	Mean	nDSM-ADS/DSM-LiDAR
Linear features	Watercourses	Watercourses >100m long.	Distance	swissTLM ^{3D} v 1.4
	Tree line	Vegetation in linear conformation (e.g. hedgerows)	Distance, Density	swissTLM ^{3D} v 1.4

¹ <http://pro.arcgis.com/fr/pro-app/help/data/imagery/curvature-function.htm>

Linear features	Roads & Railways	Roads from 1m wide to highways; railways	Distance, Dens	swissTLM ^{3D} v 1.4
Terrain	Open water	Still water	Distance, Cover,	swissTLM ^{3D} v 1.4
	Concrete ground	All land surface covered with concrete (excluding buildings)	Cover	swissTLM ^{3D} v 1.4
	Soft ground	All land surface not covered with concrete (excluding vegetation, water, buildings)	Cover	swissTLM ^{3D} v 1.4
	Slope	Terrain slope	Mean	dtm25_12
	Terrain ruggedness	Ruggedness of terrain surface calculated with 3 different methods: Terrain Ruggedness Index (Riley et al., 1999) Vector Ruggedness Measure (Sappington et al., 2007), Curvature ¹	Mean	DTM-LiDAR
	Topographic Position Index	Combined measure of slope position and landform category. See ²	Mean	tp150s
Climate	North exposure	Level of exposure to north (scaled from 0 to 1)	Mean	dtm25_12
	East exposure	Level of exposure to east (scaled from 0 to 1)	Mean	dtm25_12
	Wind exposure (North*East)	Level of exposure to main winds directions: North exposure*East exposure	Mean	dtm25_12
	Average temperature	Average of the average temperature during period of roost occupation (May-August)	Abs	Tave
	Solar radiation	Average solar radiation during period of roost occupation (May-August)	Abs	srad
Artificial light	Artificial lighting (in lux) measured at 4 points around the recording device, at a distance of ~3m for <i>R. hipposideros</i> and ~6 meters for <i>M. myotis</i> , and exactly over the device	Abs	Measured in the field	
Initial number of variables: n = 146				

² <http://www.jennessent.com/arcview/tpi.htm>

Tab. 3. Description of the measurements.

Measurement	Description
Cover	% of the surface covered by the feature at three different scales (5, 10 & 25m)
Edge	Sum of the perimeter of all the objects of this feature at three different scales (5, 10 & 25m) divided by the area
Density	Point density at three different scales (5, 10 and 25m)
Distance	Euclidian distance to the closest object of this feature
Absolute	Absolute value at sampling location
Mean	Mean value at three different scales (5, 10 and 25m)

Finding a model to predict the commuting activity of bats

We aimed to find the model which would show the best performance for predicting of commuting bats. Each species and period of activity (without & with the juveniles) was analysed separately; for this, the data were separated in four datasets (one for each species and period of activity). These datasets are referred as RH1 (*R. hipposideros*, activity period 1), RH2 (*R. hipposideros*, activity period 2), MM1 (*M. myotis*, activity period 1) and MM2 (*M. myotis*, activity period 2). Each of these sets included 360 observations (180 locations distributed at the six sites for each species, with two passages for each period of activity). For each combination of species and period of activity, we aimed to find the model that would show the best performance for predicting the activity of commuting bats.

Commuting activity of bats at each location was the response variable. It was defined as the sum of bats counted at this location during the night, a “count” being an individual acoustic sequence that had been attributed to the species after analysis of the calls. We focused on two periods during the night: the “fly-out”, when most of the bats leave the colony for foraging as soon as light conditions allow it at nightfall; and the “fly-back”, when most of the foragers come back to the roost at dawn. These peaks were generally easily identifiable when counts

were plotted against time (Fig. 4). Duration was similar for the two peaks. After visual analysis, we selected the counts taken during a period of 90 minutes (*R. hipposideros*) and 120 minutes (*M. myotis*) after the first recording (fly-out peak) and before the last recording (fly-back peak), respectively. For simplification, these two periods are referred as “commuting periods” in the text.

Treatment of the predictors

For the analyses, predictors were standardized (mean=0, standard deviation=1). In order to avoid redundant information, correlation among the predictors was inspected (Pearson Correlation test). If the information provided by two predictors was almost identical ($r > 0.95$), only the predictor that was the easiest to measure was retained. Predictors that contained more than eighty per cent of “zero” values were also eliminated, as they were not considered as informative. As a result, 90 variables were kept for model selection for *R. hipposideros*, and 96 for *M. myotis*.

Model selection

To facilitate the understanding the analyses, Fig. 3 summarizes the successive steps described here. Considering the high dimensional setting of the environmental predictors set ($p = 90$ and 96), we decided to use an automatic model selection method to find the most relevant variables. We used the Least Absolute Shrinkage and Selection Operator (LASSO) for model selection (Tibshirani, 1996). LASSO is a method based on L1-penalization, therefore applying a constraint on the sum of the coefficients absolute values. Like other shrinkage methods, it shrinks the coefficients of the less important variables towards zero, but it has the particularity to even set some coefficients to zero, hence allowing variable selection. The penalization parameter is referred as λ and defines the level of penalization. For example, a high λ induces high penalization – only the coefficients of the strongest predictors are

retained and the other ones are shrunk to zero – whereas a lower λ imposes smaller penalization – the shrinkage is smaller, and fewer coefficients are set to zero. Applying LASSO allows obtaining a reduced model retaining only the variables with the strongest relationship with the response. This method was particularly convenient for our analysis for several reasons. LASSO can perform model selection even when the number of predictors (p) is high regarding the number of observations (n) (e.g. when p similar or even greater than n); in our case, the initial number of predictors ($p=90$ and 96) was about one third of the number of observations for each set ($n=360$). Secondly, it can deal with groups of highly correlated variables, by selecting only one within each group and excluding the other ones (Oyeyemi et al., 2015; Zou and Hastie, 2005). We assumed that our variable set would include such groups, e.g. because features calculated at the three scales would sometimes result in three collinear variables, or because using two different data sources to calculate two times a variable would occasionally result in a very similar output. We expected that the LASSO would be able to efficiently avoid selecting together highly correlated variables, which would help to reduce model dimensions. Thirdly, the penalization of the coefficients usually results in smaller prediction error when compared with non-penalizing methods, as it reduces the variance of coefficient estimates and thus help to prevent overfitting (Dusen, 2016; McNeish, 2015). This propriety is shared with other shrinkage methods, such as Ridge Regression.

In LASSO, the optimal penalization parameter (or optimal λ) depends on the desired proprieties for the final model. In our case, we defined that the optimal λ should select the best predictive model, and thus maximize the predictive performance (defined in the next section). We defined the optimal λ for each dataset (referring to RH1, RH2, MM1 and MM2) by cross-validation, using internal evaluation sets. Each dataset was partitioned into six training and testing sets: five sites were used as training set, and one site was kept as independent testing set. The procedure was repeated six times, each time one different site

being used as testing set. Each training set was used to perform a prediction on the corresponding testing set, and the predictive performance was measured. These pairs of training and testing sets are referred as evaluation sets.

We used a Poisson generalized linear mixed-effects model (GLMM) with bat activity (counts) as response variable. All environmental predictors were used as explanatory variables. To account for the hierarchical structure of the data, we used the function `glmmLasso` from the `glmmLasso` package (version 1.4.4), allowing the application of LASSO to Generalized Linear Mixed Models (Groll and Tutz, 2014; Groll 2016). Analyses were conducted in R 3.3.2 (R Core Team 2016). For each training set, we applied a series of different penalization values (referred as λ *sequence*), starting from absolute constraint (all coefficients were set to zero) and gradually decreasing to reach $\lambda=0$ (no penalty). The λ sequence had to be defined for each dataset; the method that was used is described in the Annexe. Each λ resulted in a model (i.e. a set of variables with non-zero coefficient), which was used for prediction on the testing set with two different methods. First, directly using the `glmmLasso` object (result of applying the R function `glmmLasso` to fit a GLMM) and second, the object resulting from applying an un-restricted GLMM to the variable set that had been selected by LASSO. For the last one, we used the R function `glmer` from the package `lme4` (Bates et al., 2014, 2015). The aim was to see if predicting with a linear-regression method applying a penalization on the coefficients (here, `glmmLasso`) would perform better than a linear-regression method that does not use such penalization (here, `glmer`). We hypothesized that `glmmLasso` would outcompete `glmer` for prediction, as LASSO is expected to avoid overfitting. In `glmer`, the hierarchical structure of the data was accounted for by a random intercept for site, circle (crossed with site: each site has the same three circles with identical radii) and night (nested in site; each night level is observed in only one site). A limitation of `glmmLasso` was that it could not account for nested or crossed random effects terms in the formula. Thus, we

modelled crossed random effects for glmmLasso, with different levels for each “circle” for each “site”, and different levels for each “night” for each “Site”. After the measurement of the prediction error for the six training sets at each λ , one optimal λ was defined. We summed the prediction error of the six training sets; the optimal λ was the one with the lowest prediction error.

Measurement of the predictive performance

The metric used to measure the predictive performance was the predictive deviance. Like other widely used metrics, the Predictive Deviance reports the discrepancy between the observed and the predicted values. However, this metric explicitly depends on the assumed distribution of the data and scaled in consequence (Fahrmeir and Tutz, 2011), and thus is convenient if the error does not follow a Gaussian distribution. In the case of a Poisson distribution, the formula of the Predictive Deviance is

$$D(y, \hat{u}) = 2y \log\left(\frac{y}{\hat{u}}\right)$$

where y is the observation and \hat{u} the prediction. The log transformation allows accounting for the assumed Poisson distribution of the prediction error.

Definition of the final model for each dataset

For each combination of species and period of activity, we fitted a model with all the variables on the entire dataset (i.e. this time, including the six sites). We applied the optimal λ parameter that had been previously determined with the six evaluation sets. The resulting model was the final one. The procedure was done one time fitting a glmmLasso and one time a glmer, resulting in two final models for each species and period of activity.

Map of commuting activity

We applied the final model on a 4x4 kilometres square around the roost of each site. We predicted the number of counts at a 1-meter definition, using the final glmmLasso object. For each site, we predicted one time with the model selected for period 1 and one time with the model for period 2.

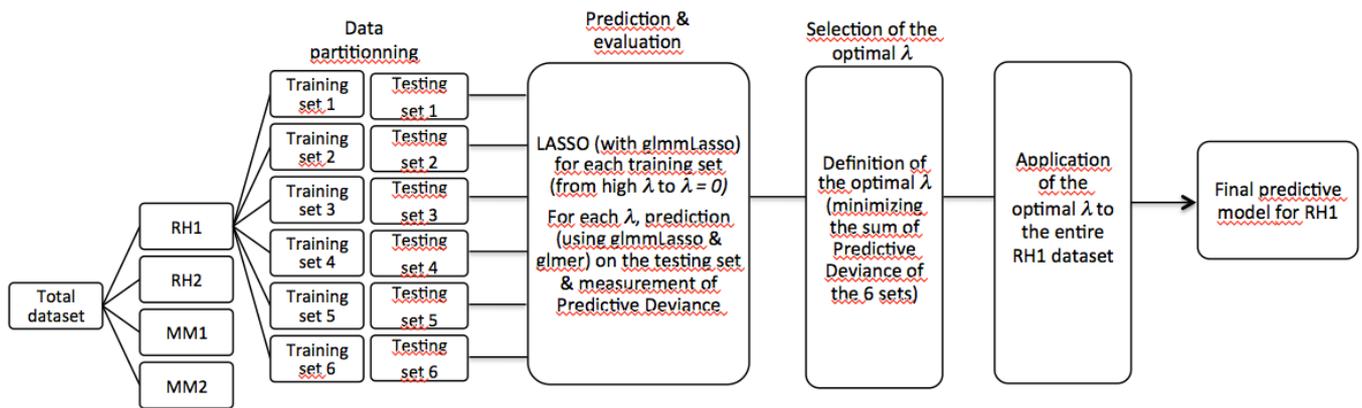


Fig. 3. Summary of the model selection steps. The procedure shown here for RH1 was repeated for each dataset.

Results

Acoustic recordings

During the 48 nights of recordings with 30 microphones, we registered a total of 348'976 sequences at *R. hipposideros* sites and 291'618 at *M. myotis* sites, during a total of 13'942 microphone recording hours. In total, 8'259 sequences were attributed to *R. hipposideros* (RHI) and 11'359 to *M. myotis* (MYM) after automatic classification, manual verification and filtering (Tab. 4). Restricted to fly-out and fly-back periods (as defined in Material & Methods; referred as “commuting periods” for simplification, see Fig. 4), we only retained 58% of the counts for RHI, and 59% for MYM. Compared to the first period of recordings (RH1 and MM1), total activity was 3.2-fold higher during the second recording period (RH2 and MM2). Hence, higher activity was recorded between commuting peaks, especially for *M. myotis* (Fig. 4). When restricting to commuting periods, counts were 2.1-fold higher during period 2 when compared with period 1. These differences were both significant (Wilcoxon Signed Ranked Test). See Tab. 4 for details per species. For each species and circle, the increase between passages 1 and 2 was significant (Wilcoxon Signed Ranked Test). The increase between periods 1 and 2 was higher at locations situated on the 60m circle than at locations on the 190 and 350m circles, especially for *M. myotis* (Tab. 5). For both species and periods of activity, counts were not significantly different between locations situated on circle a and b, and b and c for RH1, and neither between locations on circle a and b for RH1 (Mann-Whitney U test). In all other cases, counts were significantly higher at locations situated on circle a than on circle b and c, and on circle b than on circle c.

25 **Tab. 4.** summary of the counts for each species and activity period. Stars report the level of
 26 significance of the difference between period 1 and 2 (****: $P \leq 0.0001$)

Species	Activity Period	Total counts	Commuting periods (% of total counts)	Increase of counts between periods 1 & 2 in % (total counts)
<i>R. hipposideros</i>	1	2242	1571 (70%)	+ 113 % (+ 172 %) ****
	2	6119	3345 (55%)	
<i>M. myotis</i>	1	2457	2100 (85%)	+116 % (+ 263 %) ****
	2	8926	4543 (51%)	

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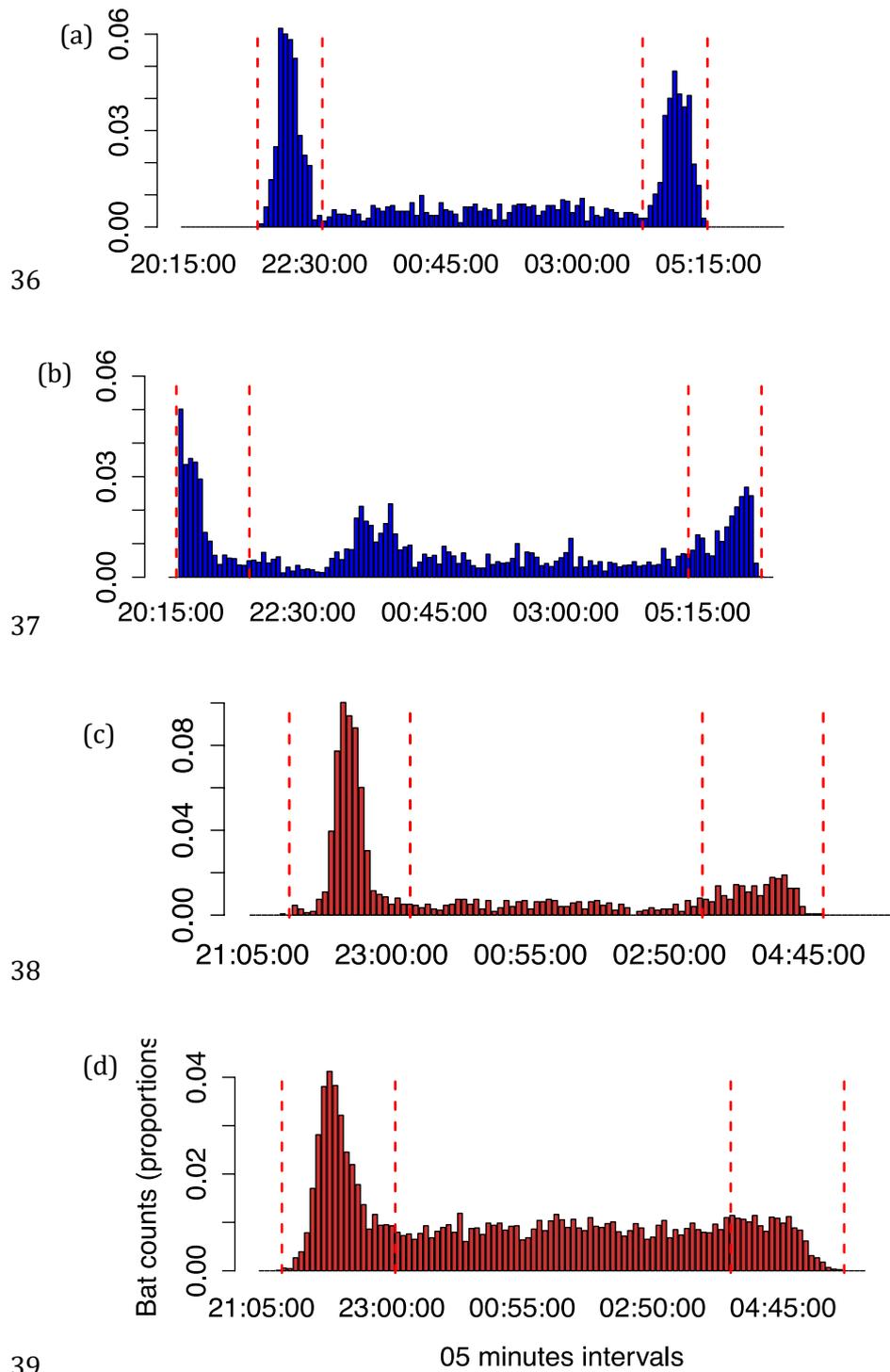
28 **Table 5:** summary of mean counts per location for each species and circle for each activity
 29 period, only considering counts during commuting periods. Standard deviation is given
 30 between brackets. Increase between period 1 and 2 is given in mean count and in percent.
 31 Stars report the level of significance of the difference between period 1 and 2 (****: $P \leq$
 32 0.0001).

Species	Activity Period	60m circle	Increase between 1 & 2 (sd)	190m circle	Increase between 1 & 2 (sd)	350m circle	Increase between 1 & 2 (sd)
<i>R. hipposideros</i>	1	7.2 (14.8)	+ 8.9 (28.9) + 120 % ****	4.4 (10.1)	+ 5 (15.4) + 109 % ****	3.4 (12.7)	+ 3.3 (17.9) + 96 % ****
	2	15.9 (32.3)		9.2 (18.3)		6.7 (20.0)	
<i>M. myotis</i>	1	15.6 (26.1)	+ 23.9 (36.0) + 149 % ****	5.0 (8.9)	+ 3.5 (9.0) + 68 % ****	2.6 (6.4)	+ 2.1 (9.0) + 77 % ****
	2	39.0 (51.1)		8.4 (11.5)		4.6 (10.1)	

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40 **Fig. 4** Temporal distribution of the counts during the night represented in five minutes
 41 intervals (commuting periods are shown between red lines). (a) RH1 (b) RH2 (c) MM1 (d)
 42 MM2

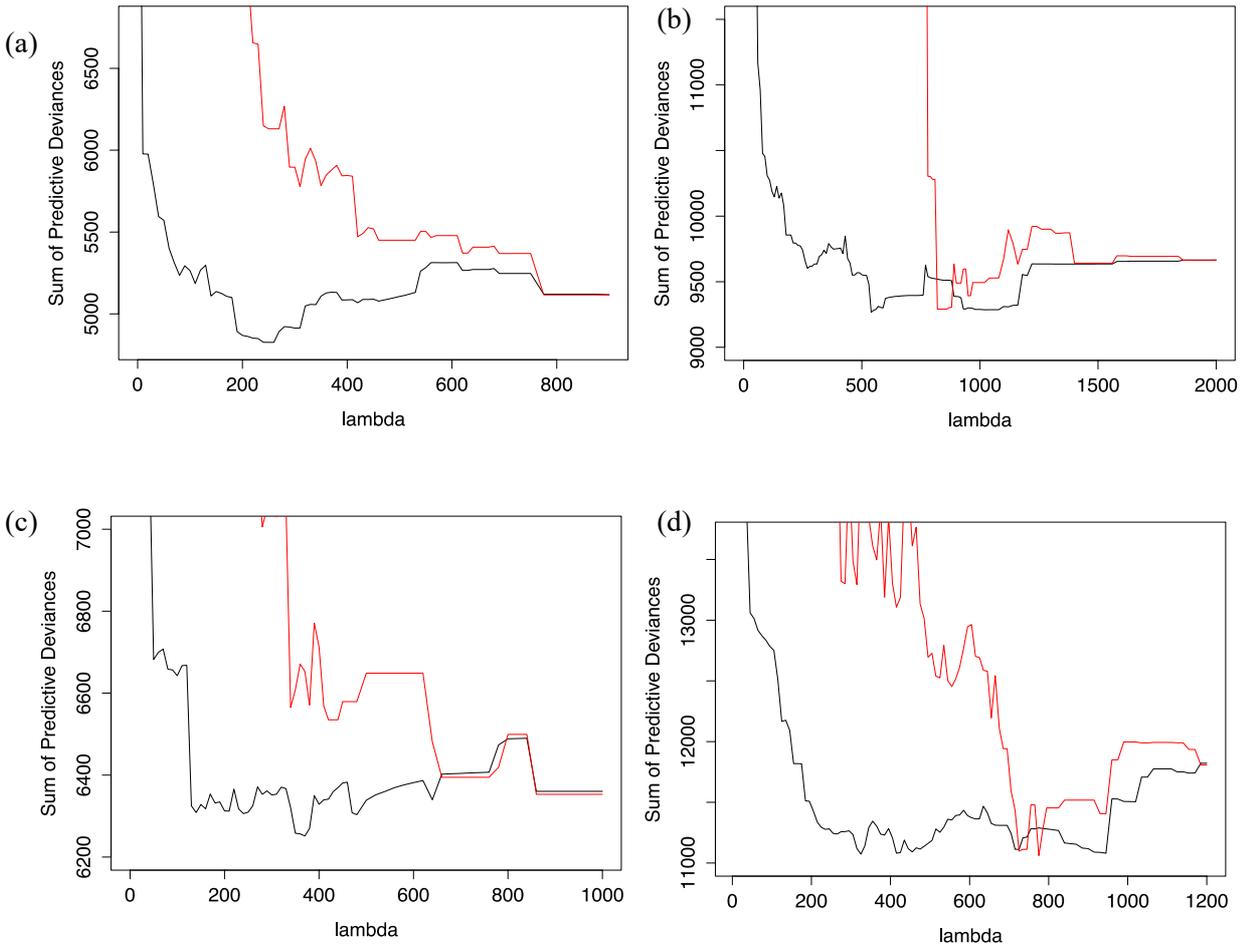
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44 *Predictive performance of glmmLasso and glmer*

45 With regard to the Predictive Deviance, glmmLasso performed better than glmer for both
46 species. Figure 5 shows the sum of Predictive Deviance of the six internal evaluations for
47 each dataset (RH1, RH2, MM1, MM2). The only occasions for which glmer outperformed
48 glmmLasso were for an average λ for RH2 (Fig. 5 b), and a high λ for MM1 (Fig. 5 c). The
49 difference of Predictive Deviance between glmmLasso and glmer in favour of the first one
50 generally increased as the penalization value (λ) decreased (Fig. 5). When predicting with
51 glmer, the error of prediction strongly increased at average penalization levels (λ); it was
52 similarly reported when predicting with glmmLasso at low penalization levels. The optimal λ ,
53 minimizing the Predictive Deviance for each dataset, was always higher when predicting with
54 glmer than with glmmLasso (Tab. 6). For RH1 and MM1 with glmer, the optimal λ
55 corresponded to the highest λ , hence to a total penalization, hence no variables were selected.
56 The final model was the result of applying the optimal λ on a model fitted with the whole the
57 dataset. The size of the final model depended on the species, the activity period and the
58 GLMM method (Tab. 6). From 8 to 19 variables were retained if the optimal λ was
59 determined using glmmLasso, and from 0 (as a result of total penalization) to 19 variables
60 when using glmer.

61 When looking at the internal evaluation sets (Fig. S1 and S2), the individual courses of the
62 Predictive Deviance showed sharper and larger fluctuations with glmer than with glmmLasso,
63 especially at low penalization levels. This resulted in a globally higher stability of the
64 Predictive Deviance course for glmmLasso than for glmer. The Predictive Deviance course
65 for predictions with glmer (Fig. S1b, S1d, S2b and S2d) is often interrupted before reaching λ
66 = 0, reporting that glmer could not fit models resulting of low λ values in most cases.

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Fig. 5. Predictive Deviance as a function of the penalization parameter (λ) for each dataset (a) RH1 (b) RH2 (c) MM1 (d) MM2. The value of Predictive Deviance results from the sum of the six internal evaluation sets. Results for predicting with glmmLasso and glmer are shown with the black line and the red line, respectively.

Table 6: summary of the optimal λ and number of selected predictors for each dataset.

Dataset	glmmLasso		glmer	
	Optimal λ	Number of selected predictors	Optimal λ	Number of selected predictors
RH1	280	7	900	0
RH2	540	18	860	6
MM1	370	12	1000	0
MM2	325	22	775	3

76 *Selected predictors in the final models*

77 We selected the final models provided by glmmLasso, since it showed better prediction
 78 performance than glmer. Tab. 7 gives the list of the selected predictors in the final model for
 79 each dataset and the estimates of the coefficients with glmmLasso. More predictors were
 80 selected at period 2 than at period 1 for both species (Tab. 6).

81 **Tab. 7.** List of the selected predictors and coefficients in the final (glmmLasso) predictive
 82 model for each dataset.

Dataset	Selected predictors	β
RH1	Soft ground (Cover) (5m scale)	-0.201
	Terrain ruggedness (Vector Ruggedness Measure) (10m scale)	0.137
	Structure ruggedness (Vector Ruggedness Measure) (5m scale) (Lidar)	0.099
	Structure ruggedness (Vector Ruggedness Measure) (5m scale) (nDSM-ADS)	0.080
	Terrain ruggedness (Vector Ruggedness Measure) (25m scale)	0.068
	Soft ground (Cover) (10m scale)	-0.068
	Terrain ruggedness (Terrain Ruggedness Index) (5m scale)	0.015
RH2	Structure Height (10m scale) (n-DSM-ADS)	0.128
	Terrain ruggedness (Vector Ruggedness Measure) (5m scale)	0.089
	Terrain ruggedness (Vector Ruggedness Measure) (10m scale)	0.071
	Structure ruggedness (Vector Ruggedness Measure) (10m scale)	0.070
	Structure ruggedness (Vector Ruggedness Measure) (5m scale)	0.060
	Canopy ruggedness (Vector Ruggedness Measure) (10m scale)	0.035
	Soft ground (Cover) (5m scale)	-0.016
	Structure height (5m scale) (n-DSM-ADS)	0.003
	Structure edge Density (10m scale)	0.003
	Terrain ruggedness (5m scale)	0.001
	Canopy height (10m scale)	0.001
	Tree line (Distance to)	-0.001
	Canopy height (5m scale)	0.001
	East exposure (25m scale)	0.001
	East exposure (value at the location)	0.001
	East exposure (10m scale)	0.001
	Water body (Distance to)	0.001
	Concrete ground (Cover) (10m scale)	0.001
MM1	Artificial light	-0.380
	Trees (Edge Density) (25m scale)	0.136
	Structures (Edge Density) (10m scale)	0.086
	Trees (Cover) (25m scale)	0.071
	Terrain ruggedness (Curvature) (10m scale)	-0.071
	Structures (Edge Density) (25m scale)	0.045
	Trees (Cover) (10m scale)	0.025
	Structure ruggedness (Vector Ruggedness Measure) (10m scale) (sDSM-ADS)	0.022
	Structure ruggedness (Terrain Ruggedness Index) (10m scale) (sDSM-ADS)	0.016
	Canopy ruggedness (Vector Ruggedness Measure) (25m scale)	0.012
	Structure ruggedness (Vector Ruggedness Measure) (25m scale) (sDSM-ADS)	0.002

	Terrain ruggedness (Curvature) (5m scale)	0.001
MM2	Artificial light	-0.173
	Structure ruggedness (Curvature) (5m scale) (LiDAR)	-0.120
	Structures (Edge Density) (25m scale)	0.119
	Terrain ruggedness (Curvature) (10m scale)	-0.116
	Roads (Distance to)	0.095
	Trees (Distance to)	-0.091
	Wind Exposure (25m scale)	-0.084
	Structures (Edge Density) (10m scale)	0.078
	Building Height (5m scale)	-0.069
	East Exposure (10m scale)	-0.056
	Structure ruggedness (Terrain Ruggedness Index) (10m scale) (nDSM-ADS)	0.046
	Structure ruggedness (Curvature) (10m scale) (LiDAR)	-0.045
	Roads (Density) (25m scale)	-0.039
	Artificial trees (Distance to)	-0.012
	Concrete ground (Cover) (10m scale)	-0.012
	Structure ruggedness (Vector Ruggedness Measure) (25m scale)	0.010
	Structures (Distance to)	-0.009
	Structures height (5m scale) (LiDAR)	-0.009
	Structure ruggedness (Vector Ruggedness Measure) (25m scale) (LiDAR)	0.006
	Canopy ruggedness (Cover) (25m scale)	0.005
Structure ruggedness (Vector Ruggedness Measure) (10m scale) (nDSM-ADS)	0.002	
Roads (Density) (25m scale)	0.001	

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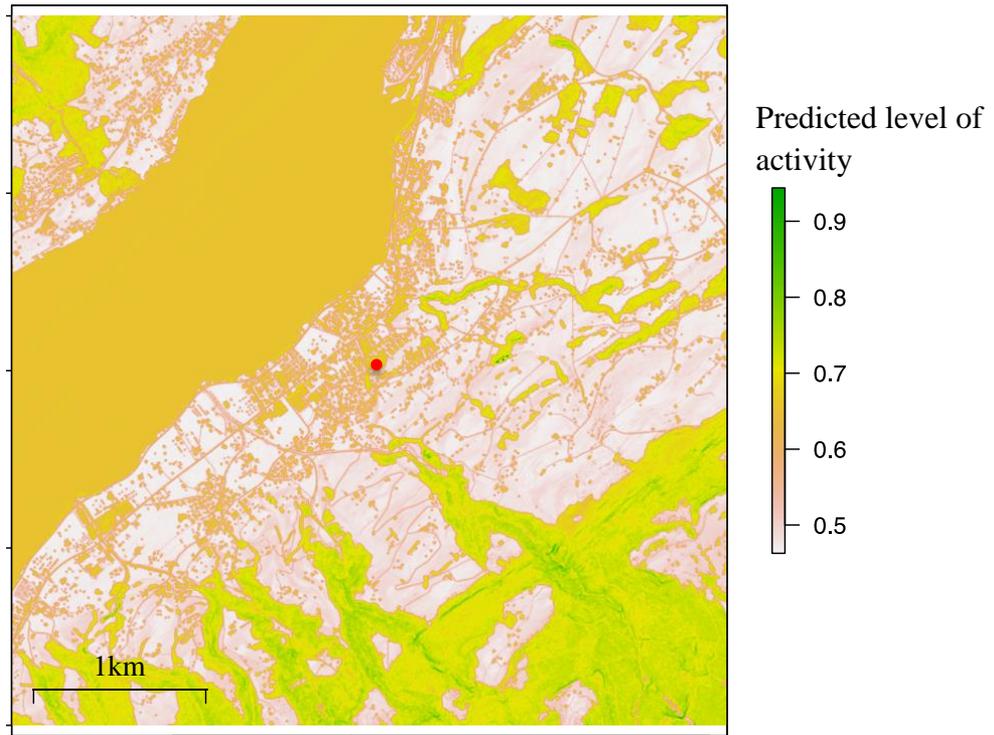
84 ***Prediction of commuting activity on a map***

85 For *R. hipposideros*, predicted activity at period 1 was generally high for areas of vegetation
86 and hedgerows, and intermediate along vegetation (in edge situations) and in the vicinity of
87 buildings and roads (Fig. 6a). At period 2, commuting activity was explicitly higher along
88 linear features such as hedgerows or vegetation patches than for other landscape features (Fig.
89 6b). For *M. myotis*, activity at period 1 was also higher for vegetation areas, but intermediate
90 level of activity was still observed for open areas such as meadows or crops (Fig. 7a). At
91 period 2, high activity levels extended to settlements, and along roads (Fig. 7b). When
92 comparing the two species, patterns of high and intermediate levels of activity were narrower
93 for *R. hipposideros* than for *M. myotis*, e.g. being more restricted to vertical structures and
94 generally low in gaps between them.

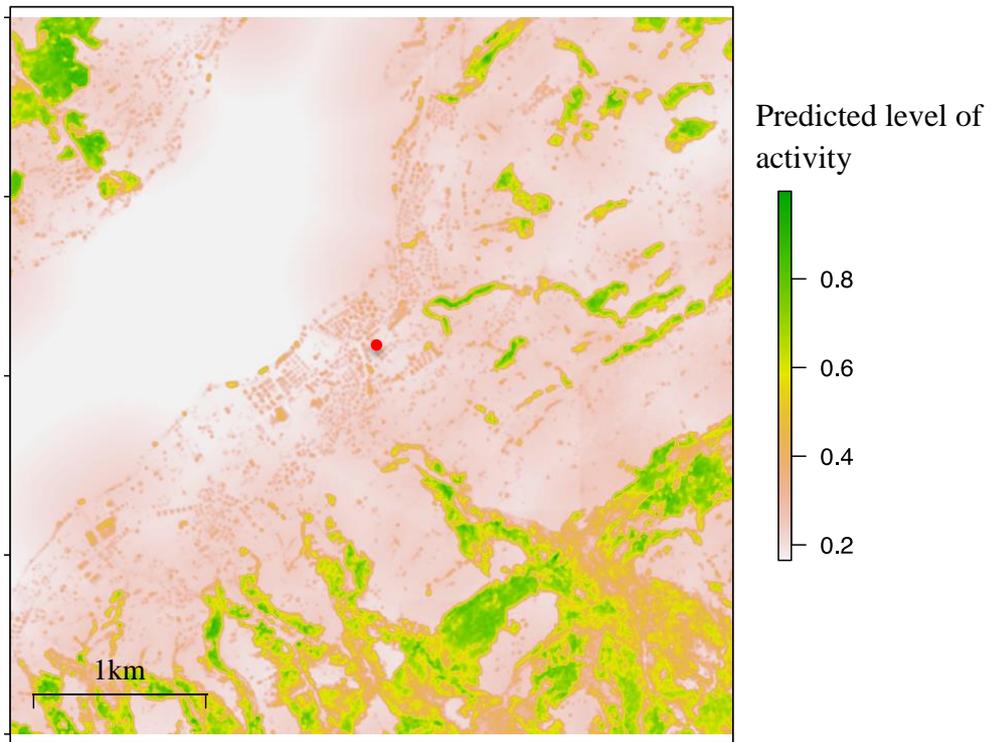
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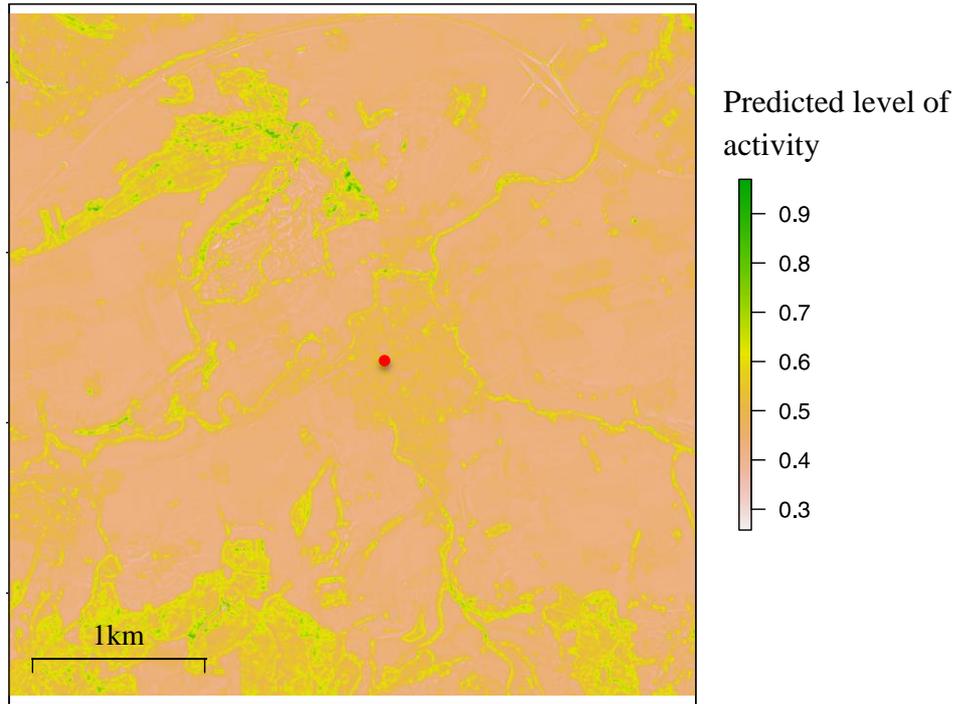


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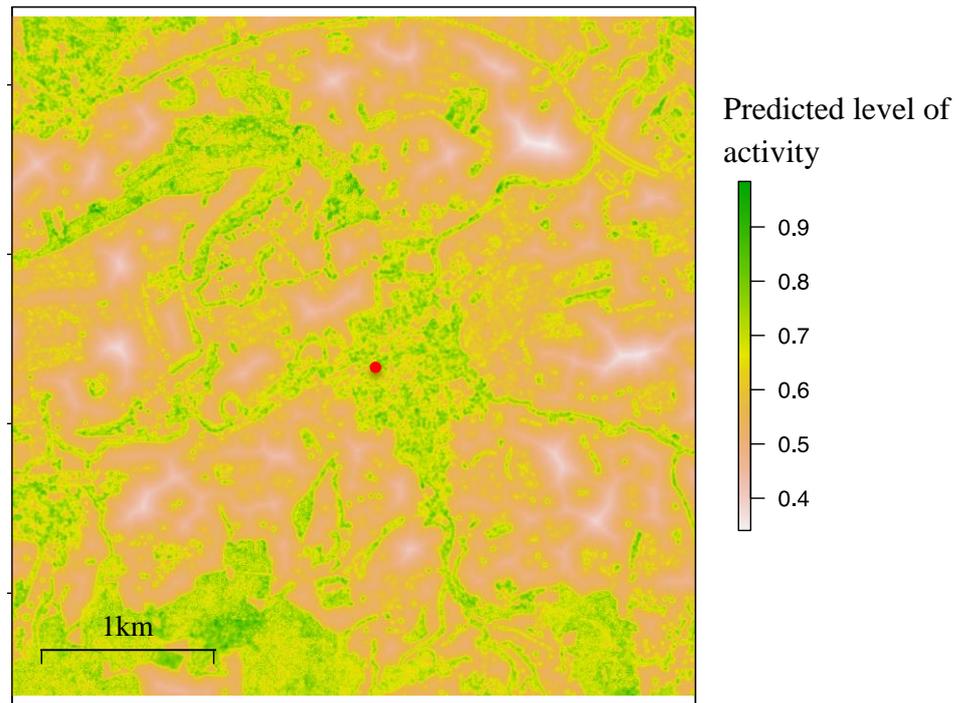


99 **Fig. 6.** Predicted activity of *R. hipposideros* at site 6 (roost=red dot) (a) RH1 (b) RH2

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103 **Fig. 7.** Predicted activity of *M. myotis* at site 7 (roost=red dot) (a) MM1 (b) MM2

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Discussion

109 *Model selection with glmmLasso*

110 For both species, model selection based on the predictive performance of glmmLasso or a re-
111 fit with glmer allowed to largely reduce the initial set of predictors, from 90 and 96 predictors
112 to less than 20. Our initial variable set included many related variables, e.g. resulting from the
113 same measurement taken at three different buffer distances (5, 10 and 25 meters), from
114 different measurements used to represent a similar landscape characteristic (e.g. the different
115 metrics used for terrain and structures ruggedness), or from same predictors calculated with
116 two different data sources (LiDAR vs Spectral data). LASSO provided an efficient automatic
117 method to select the most important variables among a large initial number, with assumed
118 high level of multicollinearity. Hence, glmmLasso provided an efficient alternative method to
119 solve high-dimensional models while using mixed effects. It has to be highlighted that the
120 relationship between the variables and the response was fitted in a rather simplistic manner, as
121 only linear relationships were considered. Since LASSO can be used for even larger settings
122 (e.g. when $p \geq n$), increasing the variable set by additionally including variables with
123 quadratic terms and still taking advantage of an efficient model selection should be possible.

124 *Comparing the predicting performance of glmmLasso and glmer*

125 The prediction performance (measured with the Predictive Deviance) was compared between
126 two types of Generalized Linear Mixed Models, one applying a penalty on the coefficients
127 (glmmLasso), and one without penalty (glmer). This comparison was done for different
128 models, resulting from a series of different penalization values (from a total penalization to a
129 non-penalized model, with gradual decreasing). As the penalization parameter decreased,
130 variables were added to the model, hence increasing model dimension. We found that
131 glmmLasso outperformed glmer with regard to the Predictive Deviance for the vast majority

132 of the models (with a few exceptions), and that this advantage increased as the penalization
133 value decreased, and as new parameters were added to the models. Additionally, the
134 Predictive Deviance course indicated that glmmLasso was less sensitive to the addition of
135 new predictors than glmer, as it showed less sharp and large variations. With glmmLasso, the
136 penalization of the coefficients allowed to “smooth” the effect of including new predictors in
137 the model, whereas, in standard GLMMs, estimates of the coefficients tend to be rapidly
138 unstable when the number of predictors increases. This advantage had already been
139 demonstrated by previous examples (Groll and Tutz, 2014), and can be especially interesting
140 when high multicollinearity is expected (Mahajan et al., 1977). glmmLasso was only showing
141 indications of overfitting for very low λ , whereas glmer already overfitted at intermediate λ .
142 The suitability of using shrinkage methods to avoid overfitting was already shown by
143 previous studies (Dusen, 2016; McNeish, 2015). Our results confirm that adding a penalty on
144 the coefficients may allow avoiding the instability of un-penalized linear regression models.

145 *Prediction of commuting activity*

146 Even if the aim of the study was not to understand the relationship between the environmental
147 predictors and the commuting activity of bats, predictive modelling can be a useful
148 exploratory tool to reveal new potential predictors (Shmueli, 2010). We review here the
149 environmental predictors that were selected to predict commuting activity, and highlight new
150 contributions in the knowledge of commuting bats. We want to emphasize that the
151 coefficients presented in Tab. 7 should be interpreted with caution. We state this from the fact
152 that LASSO generally sacrifices a little bias on the estimates to reduce the variance of the
153 prediction (Tibshirani, 1996). Additionally, since glmmLasso does not provide any p-values,
154 it is not possible to infer the strength of the relationship between the predictors and the
155 response. Hence, these coefficients should be considered as indications of the importance of
156 the predictors within the selected set.

157 As already mentioned, the commuting habitat of bats is poorly and superficially described.
158 Here, model selection highlighted that several predictors reporting 3-dimensionnal
159 characteristics of landscape features had an effect on commuting bats, as they were included
160 in the four models. For *R. hipposideros*, metrics reporting Terrain and Structures Ruggedness
161 where selected to predict the commuting activity at period 1 and period 2. For both periods,
162 the amount of open space (Soft ground) was also selected and seems to have a negative
163 effect.. It was already known that this species is adapted to foraging in highly cluttered space
164 (Schnitzler and Kalko, 2001), and that the characteristics of its echolocation signal only allow
165 for a very small detection range (Stilz and Schnitzler, 2012). Our results also suggest that for
166 *R. hipposideros*, navigation on commuting flyways is related to the spatial arrangement of
167 vertical landscape features, and certainly avoids open situations. These conclusions may also
168 be valid for others species with similar echolocation characteristics. It has to be precised that,
169 for this species, the effect of artificial light could not be tested, since the amount of sites
170 exposed to lighting was not sufficient.

171 The activity of *M. myotis* was best predicted when including Artificial lighting, Structures
172 density, and different measurements of Structures and Terrain Ruggedness and Trees for both
173 periods. As artificial light shown a negative effect on commuting activity, these results
174 provide a supplementary indication of the potential disturbing effect of light pollution on
175 commuting bats. At period 2, several other predictors were included (Roads, Wind exposure,
176 Buildings). Therefore, this species also seems to be related to vertical landscape features, and
177 sensitive to their spatial arrangement.

178 Our findings support that bat habitat should be modelled considering fine-scale environmental
179 parameters, as already proposed in other studies that assessed the relationship between bat
180 activity and complex three-dimensional forest settings (Froidevaux et al., 2016; Jung et al.,
181 2012). These precedent works hypothesized that spatial heterogeneity increased opportunities

182 for roosting and foraging. It was also proposed that flight adaptation (wing morphology and
183 echolocation characteristics) explained that some species are rather related with parameters
184 reporting cluttered environment, whereas others are related to parameters representing open
185 conditions. Additionally, another study demonstrated that many specific parameters of the
186 background structure (e.g. the shape and the absorption capacity of the surface) have an
187 influence on the quality of the echo reflected by the surface (Stilz and Schnitzler, 2012). As
188 the effect of spatial arrangement on bats has been mainly assessed on foraging bats, our
189 results give an interesting complement, showing that three-dimensional characteristics may
190 also play a role for navigation while commuting in bats. Additionally, our results support that
191 light pollution might also disturb fast-flying species such as *M. myotis*.

192 Predictions of commuting activity on the maps highlighted continuous vegetation features,
193 such as hedgerows, riparian vegetation of forest edges as potential flyways for both species.
194 Isolated features such as groves or small forest patches might play the role of connective
195 elements if the species can cross the gaps between them. For *M. myotis*, open habitats, for
196 instance meadows or crops, still displayed an intermediate level of predicted activity,
197 reporting that this species was also recorded at open locations. Hence, it is likely that this
198 species relies on more distant landscape features as landmarks than *R. hipposideros* for
199 navigating at the landscape scale. For the last, activity was mainly distributed along
200 vegetation or artificial structures, or roads (at period 1), and sharply decreased when moving
201 away from these features, which reports its very strong relationship to linear features when
202 commuting. As reported on the maps, acoustic landmarks might not always be available on
203 the commuting routes, and it is likely that bats uses other senses in complement to
204 echolocation to find their way through the landscape. For daily trips at middle-scale, spatial
205 memory certainly represents an alternative source of information (Schnitzler et al., 2003). For
206 instance, it was shown that bats can spatially memorize pathways in familiar environments to
207 surprising degrees (Barchi et al., 2013). Vision in bats has been little assessed, but several

208 studies suggest that this sense also help for navigation in some situations (M. Gorresen et al.,
209 2015; Ruczynski et al., 2011; Williams et al., 1996). Hence, crossing “gap” situations might
210 also depend on the ability of bats to use route memory and vision.

211 It has to be highlighted that data collection restricted the studies ranges to an area of about
212 400 meters around the roost, in order to limit the gap size between adjacent sampling
213 locations. However, long-distance flyers like *M. myotis* usually commute on several
214 kilometres (Arlettaz, 1996). Hence, it is possible that either the landscape composition
215 between the study area and the prediction area differed, or species’ behaviour regarding
216 structurally guiding landscape elements could change with larger distances, which could both
217 be a potential source of bias when predicting the 4x4 kilometres extent. We would expect that
218 prediction error would have a larger extent for *M. myotis* than for *R. hipposideros* when
219 extrapolating the prediction at a larger scale. Indeed, the foraging areas of the last one are
220 usually located at less than one kilometre from the roost (Bontadina et al., 2002; Mitschunas
221 and Wagner, 2015; Reiter et al., 2012), hence the real scale of the commuting corridors is
222 rather close from the one of the study, and landscape composition should be quite close from
223 that of the study area. In particular, predictive maps for *M. myotis* displayed an intermediate
224 activity level even in totally open situations. As already mentioned, finding true “gap”
225 situations within the study area was very limited. Hence, predicting in open habitats is
226 possibly limited by the study design, since the environmental conditions at the commuting
227 scale were not full represented at the sampling locations. It is then possible that this species is
228 more reluctant to fly in open lands that predicted with our models.

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232 ***Comparison between the periods of activity***

233 For both species, there was a significant increase of activity between periods 1 and 2. This
234 was expected, as juveniles started flying in the interval between the two periods. After births,
235 the number of bats in the colony can nearly double, as each female usually delivers one
236 young. For both species, the increase of recorded activity was higher when considering the
237 whole night, than when restricting to the early and late peaks of activity, defined as
238 “commuting periods”.

239 Thus, the temporal pattern of activity changed, as the overall activity was more temporally
240 constant during the night at period 2 than at period 1. This could reflect a change in the
241 behaviour of the adults, which occurred after that the young took their independence; for
242 example, the duration of foraging trips may be shorter, since their young can feed by
243 themselves. Another hypothesis is that this constant activity was due to flights of the juveniles
244 in the vicinity of the roost during the whole night, while early and late periods of activity
245 were still mainly related to commuting behaviour of the adults, passing along to the foraging
246 grounds. For *M. myotis*, the spatial distribution of activity between circles a, b and c was also
247 modified between period 1 and 2, as the increase of activity was much larger at circle a than
248 at circles b and c. Therefore, more flights occurred in the vicinity of the roost, which could
249 result from exploration flights proceeded by the young. Possibly the young are learning to
250 navigate in the vicinity of the roost, and they do not strictly follow the same flyways as the
251 adults commuting between the roost and the foraging area. Also, it is likely that young do not
252 yet have the same navigational ability as their parents. Navigation using echolocation, vision
253 and spatial memory is certainly a capacity that is acquired through learning and experience,
254 and that young have to train. For all these reasons, we can expect the use of space between
255 young and adults to differ in the beginning. When comparing the maps of predicted activity
256 for period 1 and 2, the spatial pattern of activity, was more spread in period 2 than in period 1

257 for *M. myotis*, with regard to the larger extent of high activity level. This mainly resulted from
258 higher predicted activity in the vicinity of buildings. It is possible that it is due to the activity
259 of the young at period 2, since activity increase was higher in the vicinity of the roost (Tab.
260 5), which was within the settlement for the six sites. Hence, for this species, using the data
261 collected with the young might decrease the quality of the prediction. Such difference
262 between period 1 and 2 was not observed for *R. hipposideros*, as similar activity patterns were
263 reported for the two periods. Additionally, increase of activity between period 1 and 2 was
264 similar for the three circles. These results suggest that either the behaviour of the young did
265 not differ from that of the adult, or that their activity was restricted to close vicinity of the
266 roost (i.e. less than 60 meters).

267 ***Future steps***

268 The next step of the project will be to use the predictions at landscape scale to display the
269 commuting corridors on a map. For this purpose, we will use a method based on the Circuit
270 Theory to represent the connectivity between the roost and the foraging areas. This class of
271 connectivity models is inspired from electrical circuit theory, and result in “resistance” map,
272 which highlights current flows (interpreted as ecological processes) in a landscape (McRae,
273 2008). It is an interesting alternative to least-cost path modelling, since it displays all the
274 existing possibilities to connect two areas. Another useful propriety of this method is to
275 highlight key-elements on a corridor, hence allowing detecting important connective
276 elements. It has already been applied to model landscape connectivity for a wide range of
277 species (e.g. Bennie et al., 2014; Braaker et al., 2014; Rayfield et al., 2016; Suppan and Frey-
278 Roos, 2014), and represents a useful tool for conservation biology. The predictive tool that we
279 modelled has a valuable interest for bat conservation in Switzerland and close regions, as it
280 could be widely used while only involving low computational investments. Moreover, its
281 utility could extent to other species with similar ecology.

282 ***Conclusion***

283 In this study, we demonstrated the superior prediction performance of a linear regression
284 method applying a penalization of the coefficients (glmmLasso) over a standard linear
285 regression (glmer), for different model dimensions. Cross-validation with different training
286 and (independent) testing sets was used to find the optimal penalization parameter and select
287 the best model. Model selection highlighted that, for two different species and two different
288 periods of activity, a combination of different 3-dimensionnal landscape parameters was
289 always selected, supporting that bat habitat should be modelled considering fine scale
290 structural settings, such as surface ruggedness or structure height. Finally, using the selected
291 models to predict the commuting activity in the vicinity of the study sites gave a new insight
292 of bat movements at landscape scale. The aim of the next steps of this project is to produce an
293 interpretable representation of the commuting corridors on a map, using circuit theory
294 modelling. The prediction is aimed to result in a usable tool for bat conservation measures.

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Supplementary Materials

547 *Definition of the λ sequence*

548 The λ sequence is a series of λ values (or penalization parameter) that will be applied to the
549 model. The procedure to find the optimal λ , defined as the λ that will maximize model
550 performance (in our case, predictive performance) is described in the original paper of the
551 glmmLasso package (Groll and Tutz, 2014). If a holdout set is available for directly
552 evaluating the model performance, a predictive performance metric can be used to determine
553 the optimal λ instead of using BIC or AIC (as proposed in the original method), which report
554 the goodness-of-fit of a model (with penalization on model complexity). The λ sequence
555 started with a total penalization (λ for which all coefficients are set to zero). Then, it
556 decreased regularly towards zero, and stopped only at $\lambda =$ zero. The size of the steps towards
557 zero is the main task in defining the λ sequence. In our case, we defined that ideal step size
558 should be fine enough to see the effect of new predictors added to the model, but large enough
559 to allow an easy visual interpretation of the evolution of predictive performance along the λ
560 sequence. The effect of too large steps is that many predictors (with similar importance) are
561 added to the model between two steps, and it is possible that a more parsimonious model is
562 “hidden” between two steps. But decreasing step size (and thus, increasing the length of the λ
563 sequence) increase computational time and, at some point, will result in very complicated
564 graphs, since very small variations in predictive performance are shown. A standard λ
565 sequence was tested for each of the four main set and small steps. Size of the steps was then
566 adapted to obtain interpretable graphs.

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This procedure was applied using the tools of BatScope, a software developed at the Swiss Federal Institute for Forest, Landscape and Snow Research WSL.

R. hipposideros: among sequences where *R. hipposideros* was identified, following sequences were eliminated:

- Calls with only 1 classifier agreeing
- Calls with SN < 30dB
- Calls with Peak frequency > 120kHz or < 90kHz
- Calls with Bandwidth > 50kHz

Sequence obtained were visually checked for noise.

M. myotis: among automatically classified sequences, we retained only the ones fulfilling the following criteria:

- *M. myotis* sp. as 1st species
- >50% of calls in the sequence attributed to this sp.
- >5 calls in the sequence

Then, among all the calls of these sequences, we selected following four criteria:

- Only calls attributed to the target sp.
- 3 classifiers agreeing on identification
- Recognition quality >50%
- Main call features corresponding within a 95% CI to the reference ones for this specie

572 **Table S2:** complementary information about the data sources

Data source	Data type	Source Scale	Year of measurement
swissTLM ^{3D}	3D Vector Dataset	Various	2009-2013
DTM- LiDAR DTM ³	LiDAR (High precision terrain model)	2 meters	2000-2008
VHM	Digital Vegetation Height Model	1 meter	2007-2012
dtm25_12 ⁴	Digital Elevation Model	25 meters	1994
nDSM-ADS	Digital Surface Height Model)	1 meter	2007-2012
tp150s	Topographic position	25 meters	1994
DSM-LiDAR ⁵	DOM: High precision digital surface model	2 meters	ongoing
SHM	Structure Height Model	1 meter	2007-2012
Tave	Mean summer temperature (May-August)	25 meters	1961-1990
srad	Mean monthly potential shortwave radiations (May-August)	25 meters	1961-1990

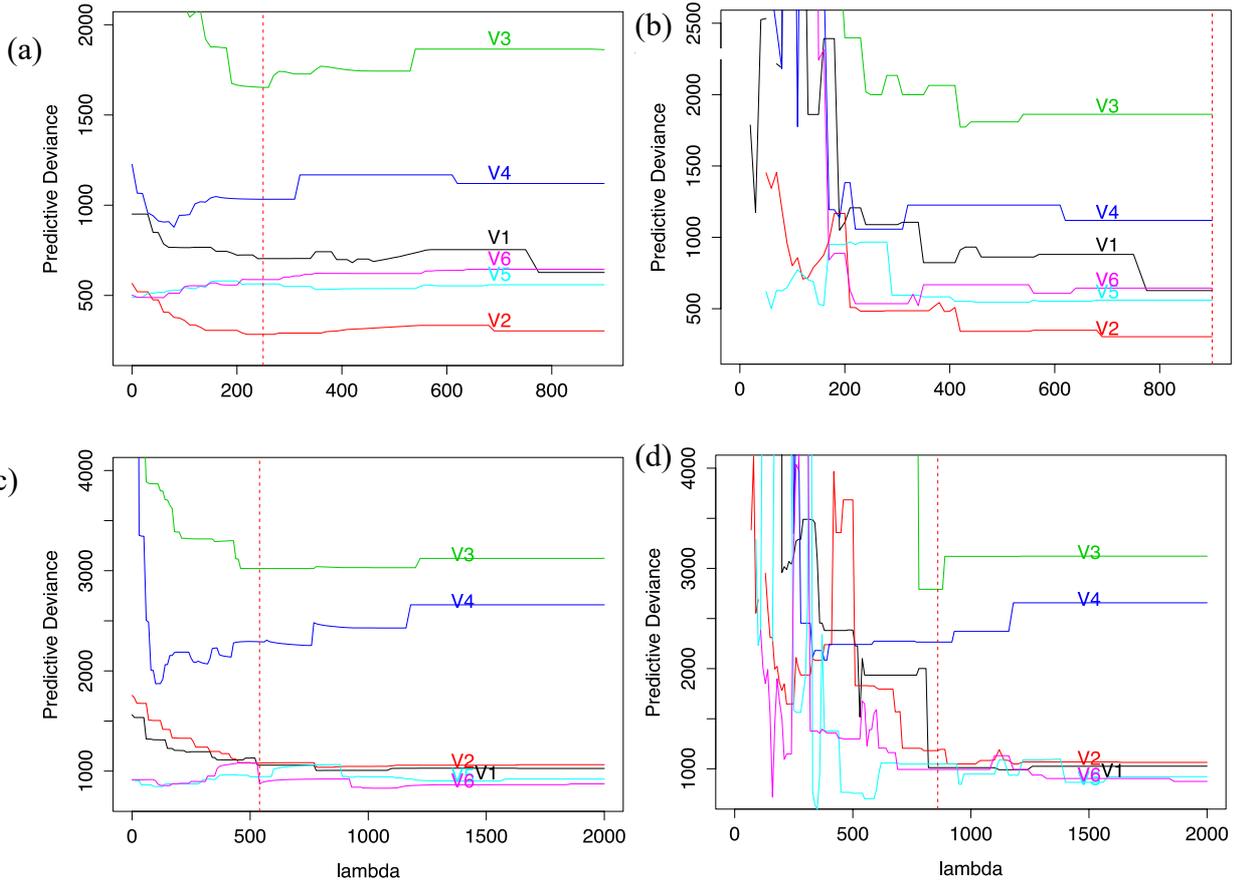
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³ Kartendaten: DTM-AV DOM-AV © 2017 Eidg. Vermessungsdirektion (DV033531)

⁴ Kartendaten: dhm25 © 2017 swisstopo (5704 000 000)

⁵ Swiss Federal Office of Topography

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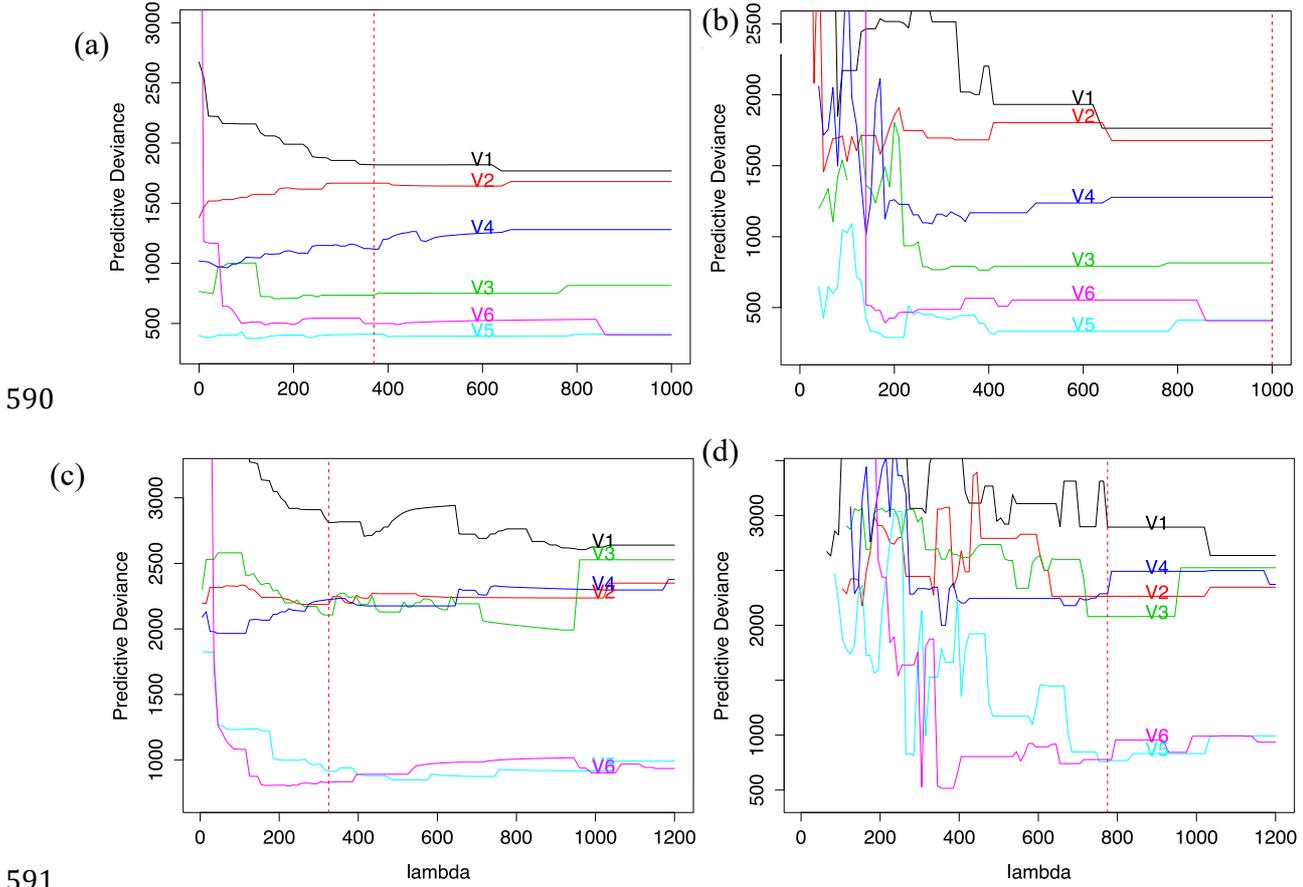
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Fig. S1. Predictive Deviance as a function of the penalization parameter (λ) for the six evaluation sets of RH1 and RH2. (a) Prediction with glmmLasso for RH1 (b) Prediction with glmer for RH1 (c) Prediction with glmmLasso for RH2 (d) Prediction with glmer for RH2. Red dotted line: λ with the smallest associated sum of Predictive Deviance (optimal λ).



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Fig. S2. Predictive Deviance as a function of the penalization parameter (λ) for the six evaluation sets of MM1 and MM2. (a) Prediction with glmLasso for MM1 (b) Prediction with glmer for MM1 (c) Prediction with glmLasso for MM2 (d) Prediction with glmer for MM2. Red dotted line: λ with the smallest associated sum of Predictive Deviance (optimal λ).

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