Understanding bat-habitat associations and the effects of monitoring on long-term roost success using a volunteer dataset

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In gregarious species, the choice of colony location is especially crucial as the costs associated with breeding near conspecifics are important and the quality of a breeding patch is known to affect individual fitness. Consequently one could expect robust decision-making rules regarding colony location. The conceptual framework of animal aggregation with regards to habitat selection emphasizes that the presence and success of conspecifics are cues to habitat selection. Based on this, we explored how the distribution of breeding colonies could inform us about how habitat selection operates in bats. The data set we used was provided by a volunteer network whose first aim is to advise citizens facing bats in distress or bats in their homes. The dataset contained information on the locations of 105 serotine (*Eptesicus serotinus*) breeding colonies in a French region primarily dominated by an agricultural landscape. The methodology used for calculating habitat availability was based on the comparison of habitats surrounding serotine colonies to habitats surrounding random points. We found that serotine bats positively select pastoral and aquatic habitats regardless of the comparison used. The strong correlation between our results and those obtained with radio-tracking or acoustic methods underlines the robustness of this spatial distribution approach. The analysis of the history of the serotine colonies over a period of nearly 20 years showed that when attics are restored by the owners without the help of the bat rescue network, the probability of a departure of colony is greater. In addition, monitoring reduces the occurrence of an unsympathetic building restoration.

Key words: habitat selection, distribution, local wildlife, protection, *Eptesicus serotinus*

Introduction

Although legally protected in European countries through national or European laws (Council Directive, 1992; Convention on Migratory Species, 1985–2008, and Agreement on the Conservation of Populations of European Bats), many European bats are endangered throughout much of their range (IUCN, 2011). Numerous causes of this situation have been identified and include the availability of suitable foraging habitats (Walsh and Harris, 1996; Kunz and Fenton, 2003), agricultural practices that use toxic pesticides (Dunsmore *et al*., 1974; Swanepoel *et al*., 1999; Wickramasinghe *et al*., 2004), emerging infectious diseases (Frick *et al*., 2010; Puechmaille *et al*., 2011), and roost destruction and disturbance (Mitchell-Jones *et al*., 2007). However, land use changes are often considered to be the principal cause of population decline in many bat species

(Battersby, 2010). The life history of bats is characterized by low fecundity and high longevity, and this K-strategy has been selected in a stable environment. Thus, bats are particularly vulnerable to environmental changes that lead to reduced demographic parameter values (Walsh and Harris, 1996; Kunz and Fenton, 2003). Therefore, an accurate description of the habitat requirements of threatened species, such as bats, is a key part of conservation management (Walsh and Harris, 1996).

The great majority of studies dealing with habitat preferences have been based on intensive protocols, such as radio-tracking (Robinson and Stebbings, 1997; Goiti *et al*., 2003; Davidson-Watts *et al*., 2006; Flaquer *et al*., 2008). These methods often involve animal handling, such as capture during mist-net sessions, which can be controversial approaches when species are endangered and/or sensitive to disturbance. This is particularly the case for

bats (Dietz *et al*., 2006; A. Punt, in litt.). In addition, these studies are often limited in space and time and involve a restricted number of individuals (Boughey *et al*., 2011). Complementary acoustic detection methods have been developed to describe foraging habitats (Carmel and Safriel, 1998; Shiel and Fairley, 1998; Rainho, 2007). However, despite the quality information they produce, these two approaches (radio-tracking and acoustic) are time-consuming and require highly qualified people.

Due to the awareness of biodiversity loss, there is a pressing need for amateur naturalist volunteers to participate in data collection for biodiversity monitoring programs in Europe (Bell *et al*., 2008). Thanks to citizen scientists, studies can be carried out despite small budgets. Thus, the conservation initiatives and biodiversity studies carried out each year are numerous (Henry *et al*., 2008), while the budgets for biodiversity conservation are scattered and scarce. We need to better exploit the information contained in studies and field conservation experiences (Sutherland *et al*., 2004) and judge the effectiveness of conservation interventions in different contexts to ensure that the scarce funds go as far as possible toward improving our knowledge of the function of biodiversity to achieve conservation outcomes (Ferraro and Pattanayak, 2006).

To date, the studies investigating roost data have dealt with roost characteristics, such as the height of roost openings above ground level (Simon *et al*., 2004), exposure (Simon *et al*., 2004), external or internal temperature (Churchill, 1991; Mitchel-Jones *et al*., 2007), or hygrometric conditions (Hall, 1982). These works were primarily conducted with the aim of identifying potential roost features and thus developing efficient conservation programs, such as physical protection measures (Mitchel-Jones *et al*., 2007), the restoration of roosts during the restoration of buildings or even the creation of new roosting opportunities (Marnell and Presetnik, 2010). Surprisingly, however, very few studies have attempted to analyze spatial distribution data with the aim of identifying how habitat selection operates in bats' choice of roost (Lumsden *et al*., 2002; Boughey *et al*., 2011; Nicholls and Racey, 2011). The main reason for the lack of research on this topic is most likely related to the fact that, without a doubt, the choice of breeding site is primarily based on intrinsic characteristics (e.g., ease of access, temperature, luminosity, and humidity). In addition to this, many species are highly philopatric (Bogdanowicz *et al*., 2013); thus, one could expect that bats will return to the same breeding site year after year even if the surrounding landscape suffers some changes. However, there are important costs associated with breeding in a colony such as the increased probability of transmission of parasites (Brown and Bomberger, 1996) or diseases (Frick *et al*., 2010), the competition for space, food and mates. Thus, benefits must exist and must at least balance the cost (for more details, see Danchin and Wagner, 1997). Thus, several authors have analyzed colonial species strategies in the framework of habitat selection (Doligez *et al*., 2003). Because the choice of a breeding patch affects individual fitness (i.e., survival and reproductive success), one could expect robust decision-making rules. Numerous theoretical, experimental and empirical studies (Danchin and Wagner, 1997) have found that for colonial species, the presence and success of conspecifics are cues to habitat selection. For species that have a large number of sites available for reproduction, such as species able to use man-made aboveground structures, we hypothesize that we can detect how habitat selection operates using the spatial distribution of roosts. In contrast, exclusive cave-dwelling species potentially have much lower roost availability; thus, they most likely cannot afford to choose the roost by its surrounding habitat because it is likely a secondary endpoint compared to intrinsic characteristics of the site.

Here, we explored how the breeding colony distribution of a species using over-ground roosts (such as attic of house or church) could inform us of how habitat selection operates We used habitat variables that are available at the European level (Corine Land Cover, 2000: http://sia.eionet.europa.eu/CLC2000) and breeding colony data that was provided by a network of local bat rescue volunteers, with the aim of proposing a simple method with a high potential for generalization. Although the primary purpose of these associations is to assist and rehabilitate injured or orphaned bats, identifying the location of breeding colonies is a natural output of such volunteer network. Many non-governmental nature conservation associations aim to help every citizen facing bat-related issues such as the discovery of a colony in their home and exist in many European states (e.g., Mitchell-Jones *et al*., 2007; Marnell and Presetnik, 2010; Boughey *et al*., 2011).

We used a dataset of serotine bat (*Eptesicus serotinus*) breeding colonies to explore how their distribution could inform us about habitat selection by this species. Maternity colonies of serotine bats are known to inhabit large roof spaces (Simon *et al*., 2004; Harbusch and Racey, 2006; Vos *et al*., 2007).

This data set was provided by a regional volunteer network. We studied the environment surrounding serotine breeding colonies in a 7,300 km² French agricultural landscape and compared it to habitats surrounding randomly selected points. In addition, we assess the effectiveness of this monitoring in terms of serotine roost conservation.

MATERIAL AND METHODS

Study Areas

The Museum of Bourges coordinated the inventory of bat colonies in the Cher from 1988 to 2009. The Cher is an administrative region (7,300 km²) in the centre of France (Fig. 1) that is primarily dominated by two contrasting agricultural practices: large patches of arable land (44% of the total Cher area; average patch size: 5.1 km² ± 2.3 km²) and small patches of pasture (23% of the total area; average patch size: 2.7 km² ± 1.2 km²). Forest covers 21% of the Cher's total surface (average patch: 1.9 km² ± 0.7 km²) (sources: Corine Land Cover, 2000).

Data Collection

Volunteer network

The Museum of Bourges coordinates a network of volunteers who work on bat surveys and the local bat rescue network of this region. All volunteers were trained in the identification of bats by one of the co-authors, and in addition, the vast majority of sites have been visited in the first year of their discovery by two co-authors. This French network for bat rescue allows citizens to contact a bat expert in their region by calling a unique telephone number when they have question about bats. For example, when someone finds a bat in distress, discovers a bat colony in his home, or decides to restore a home and suspects that some bats are living here, an expert may provide legal information on bat protection status or solutions for home restoration that allow the sustainable maintenance of the bat colony. These experts often conduct private home visits and thus discover a breeding colony (Réseau SOS Chauve-souris: http://www.museum-bourges.net/chauve-souris-unreseau-d-aide-29.html.). Such networks also exist in many European countries (Marnell and Presetnik, 2010). Most of the time, when a permanent relationship is established with the owner, bat colonies are secured and surveys are performed. In the Cher, this 22-year coordination has supported the development of an impressive database that contains 724 localized breeding colonies for 14 species. Because the aim of this study was to investigate habitat selection, we only considered breeding roosts.

Serotine roosts

Serotine bats primarily choose buildings as breeding sites (Schmidt, 2002; Dietz *et al.*, 2007). The database contains 105 serotine bat colonies, 96% of which are located in attics, with the others located in bridges, in trees, in flues or behind shutters. The yearly rate of visit is 0.36 ± 0.02 SE (i.e., on average, a colony is visited every three years). We did not consider colony shifts from one house to another house (in the same village, for example) less than one km (average 300 m) away as supplementary colonies. The shift of a colony from one roost to another

occurred six times in the study period (1988–2009). Simon *et al.* (2004) also noticed small movements of breeding colonies.

Constitution of the dataset and evaluation of potential bias

Our dataset does not come from a systematic inventory but from opportunistic observations collected over a long period; thus, in our first step, we explored how the database (observations of colonies — locality and date, already known or new colonies) was built up over the years with the aim of evaluating potential bias. We used linear modelling to test the trends of discovery of new colonies ('cumulative number of colonies' as the response variable) along 'years' (the explanatory variable). We also used a Generalized Additive Model (GAM — Hastie and Tibshirani, 1990; R package 'mgcv') to test the existence of non-linear effects of the yearly trend of new colonies in the database, with 'years' as an explicative smoothed variable. As a second step, we assessed whether there were spatial and temporal biases in the implementation of this database. We tested if the discovery of a number of new colonies among regions (the study areas was split in four equal areas) was similar among periods (the study period was split in four periods: 1988–1993, 1993–1998, 1999–2003, 2004–2009) using a Chi-squared contingency table.

Habitat Selection Analyses

Before investigating the links between serotine habitat selection information and the spatial distribution of colonies, we tested the normality of colony distribution using the simple approach proposed by Clark and Evans (1954), which compares the expected mean distance to the nearest neighbor to the observed mean nearest neighbor distance.

We then tested the existence of a habitat selection process by comparing the habitat available in the study area and the habitat surrounding serotine breeding colonies ($n = 105$). With the aim of evaluating habitat availability, we inventoried habitats surrounding 105 random points used as pseudo-absence (using the random point function in ArcGis 9) by following the approaches of Jiguet and Villarubias (2004) and Boughey *et al.* (2011). Among these random points, we selected 105 points that included at least one hamlet or building in their 2 km² buffer to attempt to account for serotine colony installation requirements (see Appendix I). No obvious bias was detected in the habitat area distribution of the random point data set and global habitat proportion in the Cher region (Kolmogorov-Smirnov test, $D = 0.36$, $P = 0.078$). According to Phillips *et al.* (2009) we developed an alternative approach based on a target background approach for designing our pseudo absences: we used roost site locations of *Pipistrellus pipistrellus* which roosts in similar structures (data provide from the same data set than *E. serotinus*). Among the 411 breeding colonies of *P. pipistrellus* (Appendix I) we used 105 roosts as pseudo absences. These two species, even if they were not in mixed colonies in our case, are known to have very similar roost requirements (Simon *et al.*, 2004; Dietz *et al.*, 2007; Arthur and Lemaire, 2009; Marnell and Presetnik, 2010).

Choice of buffer dimension

The choice of the buffer size is important; if too small, the buffer may consider only a small part of the space that is potentially used by the individual of the colony. Conversely, with
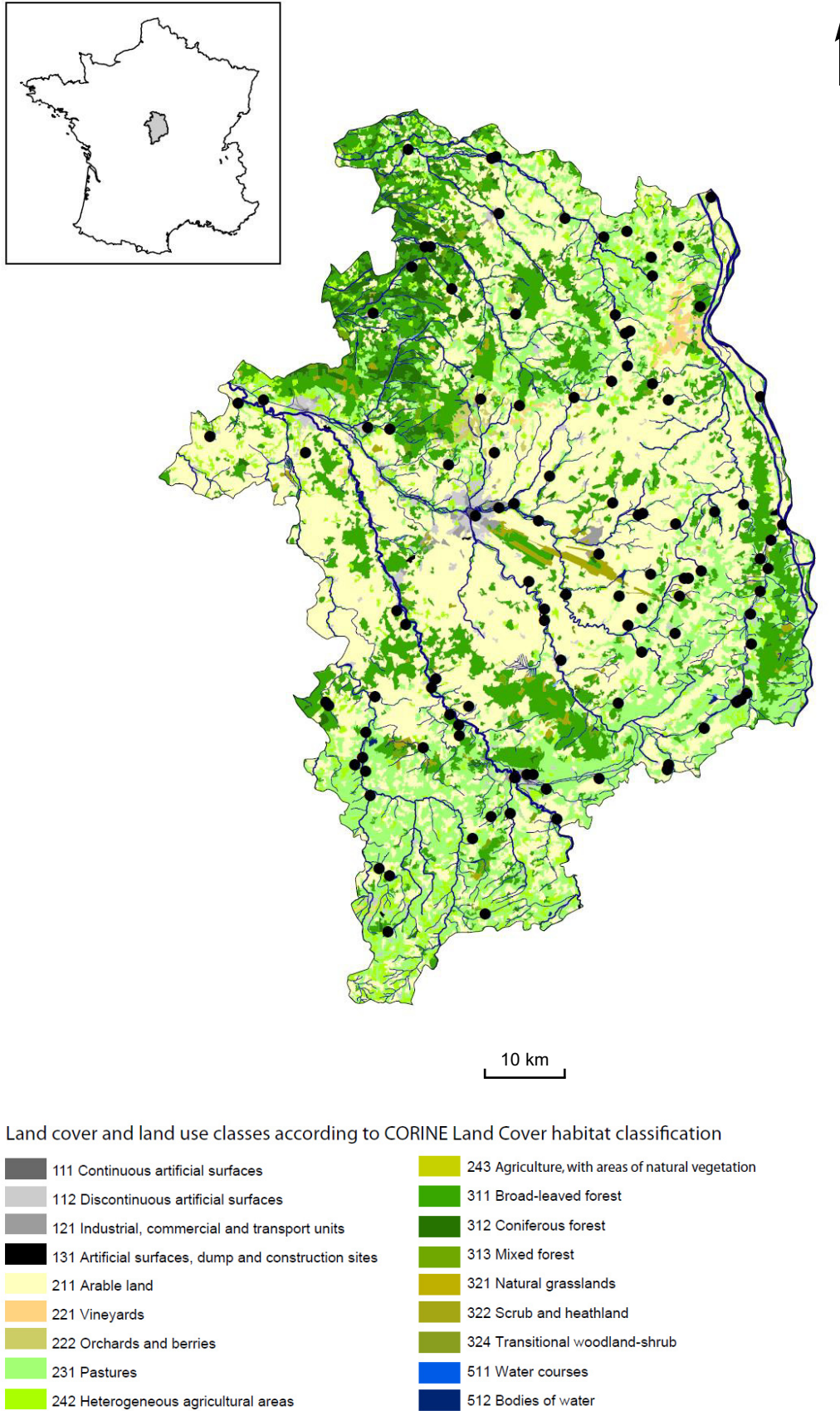
10 km

Land cover and land use classes according to CORINE Land Cover habitat classification

- 111 Continuous artificial surfaces
- 112 Discontinuous artificial surfaces
- 121 Industrial, commercial and transport units
- 131 Artificial surfaces, dump and construction sites
- 211 Arable land
- 221 Vineyards
- 222 Orchards and berries
- 231 Pastures
- 242 Heterogeneous agricultural areas
- 243 Agriculture, with areas of natural vegetation
- 311 Broad-leaved forest
- 312 Coniferous forest
- 313 Mixed forest
- 321 Natural grasslands
- 322 Scrub and heathland
- 324 Transitional woodland-shrub
- 511 Water courses
- 512 Bodies of water

Fig. 1. Geographical location of the study area (Cher), land cover use in the region and the localization of *E. serotinus* breeding colonies (●)

a buffer size that is too large, we may include many areas that are not used for foraging by breeders because of the distance to the colony. To select a buffer size that is ecologically practical, we relied on telemetry studies that were already conducted on this species. Radio-telemetry from serotine studies indicates that the distance between the breeding colony and foraging areas could reach 11.5 km (Degn, 1983; Perez and Ibañez, 1991; Diehl, 1994; Weidner, 1995; Catto *et al.*, 1996; Robinson and Stebbings, 1997; Lubeley and Bohle, 2001), but the mean distance from roost to foraging areas ranges between 1.2 and 3.6 km (Hübner, 1991; Dense, 1992; Robinson and Stebbings, 1997; Kervyn *et al.*, 1998; Lubeley and Bohle, 2001; Harbusch, 2002; Simon *et al.*, 2004). Thus, the home range of individually radio-tracked serotines was found to vary between 1.61 km² and 17.05 km² (Perez and Ibañez, 1991) and 0.16 km² to 47.58 km² (Robinson and Stebbings, 1997). The size of the home range per colony also varies considerably, ranging from > 2 km² in the study carried out by Degn (1983) to 9.4 km² (Rosenau, 2001), 16 km² (Diehl, 1994), 26 km² (Harbusch, 2002) and 19 km² for the core area of the colony in Robinson and Stebbings's study (1997). Thus, we defined 12 circular buffers (from 100 to 8000 m) around colonies or random points and hypothezise that a radius of two km wich corresponded to an approximately 13 km² area surrounding the colonies could be a good measure.

Choice of habitat variables studied

In addition to testing how habitat selection operates using the spatial distribution of roosts, we also wanted to assess the potential to generalize such a study. This is the reason why we used habitat data standardized at a large scale and with free access such as the Corine Land Cover (2000), even if such spatial information is considered relatively coarse. Hereafter, we use the habitat names used in the Corine Land Cover classification. Among the 25 habitat classes present in the Cher region, we selected the 18 most important habitats: those that had areas that represent more than 5% of the territory (Fig. 2). According to the resolution scale of the geographic information layer that we used (Corine Land Cover, CLC), the changes of land use can be considered to be minor during the study period (land cover flows in the studied region less affected than 1% of land cover; source: 1992–2006 Land Cover Flows, http://www.eea.europa.eu).

As underlined by several studies, bats in general and serotines in particular select linear elements of landscape within their foraging home range (Robinson and Stebbings, 1997; Verboom and Huitema, 1997; Waters *et al.*, 1999; Russ and Montgomery, 2002; Smith and Racey, 2008). Therefore, we also assessed the length of forest edge and the length of rivers in the 2 km² buffer areas in addition to habitat areas.

As we studied the breeding colonies, we expected a great sensitivity to the distance between the colony and foraging habitat in the serotines. The distance clearly appears to be an energetic constraint for breeding bats that must balance their night time budget between foraging in the landscape and feeding their young in the colony (Kunz and Fenton, 2003). Therefore, we also included the distance to the nearest wood, pasture, and river in our analysis and the number of the confluence of two rivers within the buffer. So, in total, for each buffer, we have 24 variables: 18 variables that are surfaces of habitats (CLC class, m²), three variables are distances to habitat (pasture, river, wood), two variables that are linear densities (edge forest and river, m) and one variable that is the number of river confluences.

Statistical Analysis

We tested differences in habitat distribution between the surroundings of serotine colonies and the surroundings of random points using Generalized Linear Models (GLM). According to the nature of our response variable (presence/pseudo-absence), we used a binomial error distribution with logit link. Our explanatory variables were habitat areas present in the 2 km² buffer (areas were log transformed). According to numerous correlations between habitats (Spearman rho > 0.5), such as the negative correlation between arable land and broad-leafed forest (Appendix II), we analyzed the differences in habitat distribution between serotine colonies and random points, habitat by habitat (i.e., 18 models), thus avoiding multi-colinearity problems. To account for spatial autocorrelation, we added an autocovariate (i.e., a distance-weighted function of neighboring response values — Dormann *et al.*, 2007; Penone *et al.*, 2013) with the autocov dist function in R (package 'spdep' by Roger Bivand). Our statistical models were structured in the following way:

$$[\textit{Presence/pseudo-absence}] \sim \textit{Habitat}_i + \text{autocovariate}$$

where $_i$ is one of the 18 selected habitats. The results were expressed using a *F*-test and accounting for over-dispersion by following the Faraway (2006) and Crawley (2009) approaches.

Beyond the identification of differences in habitat distribution between the surroundings of serotine colonies and the surroundings of random points, we tried to assess which differences are the most significant. In this second step, we simultaneously took into account all habitat variables in the analysis using Hierarchical Partitioning (HP, R package 'hier.part' by Chris Walsh), a multiple regression analytical method that allow us to identify the most likely causal factors while alleviating multicollinearity problems (Mac Nally, 2000). Based on Olea *et al.* (2010), commenting on HP usage limits, we limited this partitioning to the nine most important habitats.

In a third step, because the choice of buffer size is important for this study, we evaluated whether the scale choice based on the ecology of the species was efficient and because the species responds to its environment on a range of scales (Boughey *et al.*, 2011), we performed a multiscale habitat association study using GLM. We used the same response variable (presence/pseudo-absence of serotine roost) and a restricted set of habitat variables chosen to be significant for discriminating *E. serotinus* roosts and random points (results of the two previous steps) without exhibiting important correlation (Appendix II). Our statistical models were structured in the following way:

$$[\textit{Presence/pseudo-absence}] \sim \textit{Habitat}_i + \textit{Habitat}_j + \textit{Habitat}_k + \ldots, \text{autocovariate}$$

We ran these models with different buffer sizes, from a radius of 100 m around colonies or random points to 8,000 m. Habitat areas were expressed as a percentage of areas within the buffer. As in the first step, we included an autocovariate function and used a binomial error distribution with logit link. To adjust the effect of each variable to the effects of other variables, test values were expressed using type-II ANOVA (R, package 'car' by John Fox). Type II tests are calculated according to the principle of marginality, each term is tested after all others (Crawley, 2009), and we take into account over-dispersion.
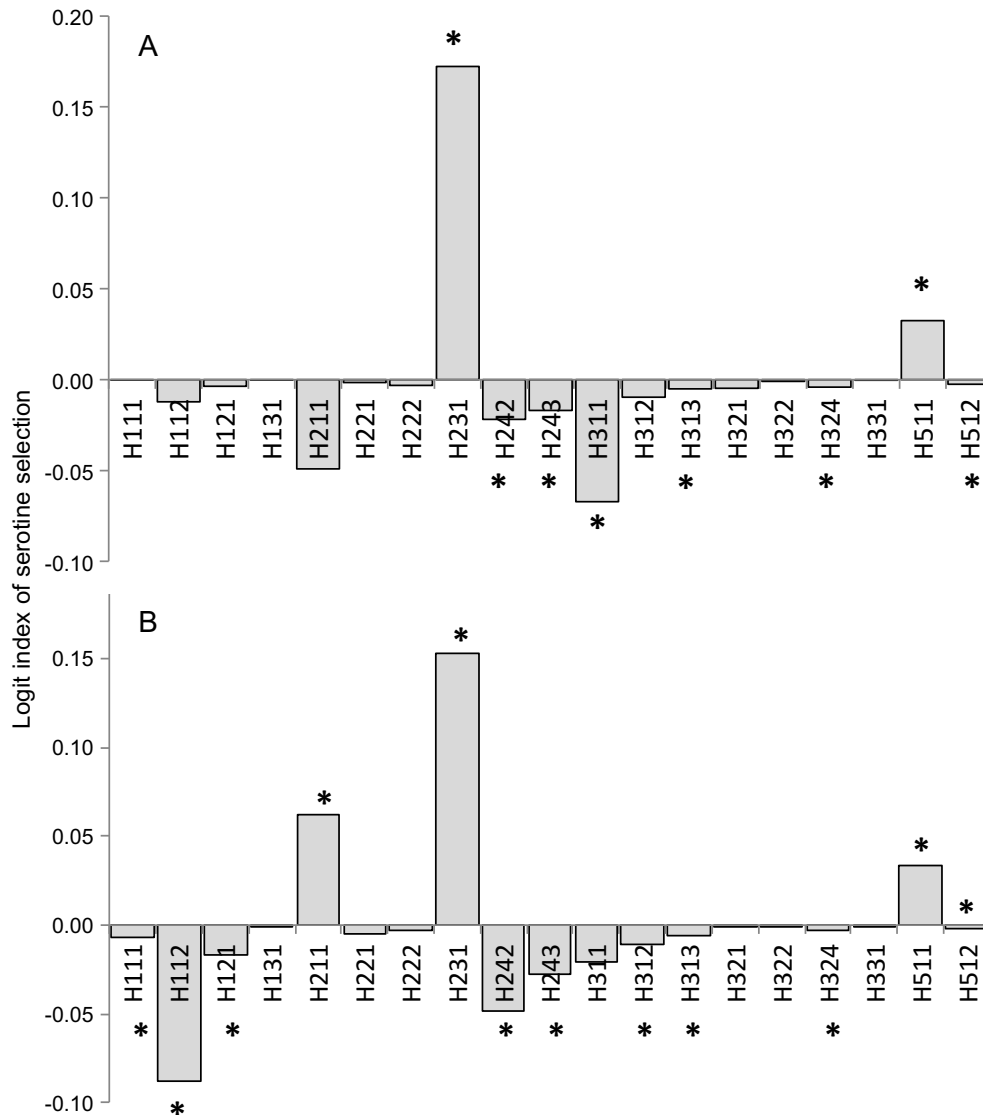
FIG. 2. Differences in a 2,000 m habitat selection radius between (A) serotine roost and random points, and (B) serotine roost and pipistrelles roosts. Significant differences ($P < 0.05$, see also Appendix III) are indicated with an asterisk (*). Corine Land Cover habitat typology: H111 — Continuous artificial surfaces, H112 — Discontinuous artificial surfaces, H121 — Industrial, commercial and transport units, H131 — Artificial surfaces, dump and construction sites, H211 — Arable land, H221 — Vineyards, H231 — Pastures, H242 — Heterogeneous agricultural areas, H243 — Land principally occupied by agriculture, with significant areas of natural vegetation, H311 — Broad-leaved forest, H312 — Coniferous forest, H313 — Mixed forest, H321 — Natural grasslands, H322 — Scrub and heathland, H324 — Transitional woodland-shrub, H331 — Open spaces with little or no vegetation, H511 — Water courses, H512 — Bodies of water

Effectiveness of this Monitoring in Terms of Serotine Roost Conservation

Such networks involving citizen-landowners have resulted in the establishment of frequent and permanent relationships with the owner. Hereafter, we assess the effectiveness of this relationship in terms of the sustainability of serotine roosts in the long term (when landowners plan to work in their attics or the renovation of heritage buildings, etc.).

Using Generalized Linear Models (GLM with binomial error distribution), we attempt to identify which factor could influence the sustainability of serotine roosts: changes in facilities (type of facilities were ranked from soft to important in four classes, i.e., from changes some tiles to total reroofing, and a fifth class in cases where there is a deliberate attempt to remove the colony) that plans and designs the work of building restoration (Museum of Bourges versus landowners) and the year and the size of the serotine population. We used the database of the history of serotine colonies ($n = 105$) over a period of 22 years, including 48 events of work in buildings sheltering serotine colonies. Test values were expressed using type-II ANOVA (R, package 'car'). All of the analyses were computed with R software (R Development Core Team, 2010).

RESULTS

Evaluation of Spatial and Temporal Biases in the Establishment of the Database

During the colony inventory period (1988–2009), we detect a significant continuous annual growth in the inventoried serotine colonies (an addition of five colonies/year, $R^2 = 0.99$, $F_{1, 20} = 2581.80$, $P \ll 0.001$). No non-linear effects were detected (GAM, $F_{1, 20} = 1.21$, $P = 0.33$). To evaluate the possibility of a bias in the accumulation of space and time data, we split the Cher region into four equal areas and split the time series into periods of four years. We did not detect any obvious bias in the location of new colonies across any time period ($\chi^2 = 10.87$, $d.f. = 12$, $P = 0.54$).

Habitat Selection Analyses

The density of the serotine colonies observed in the study area was $0.01/\mathrm{km}^2$. The comparison of the actual mean nearest neighbor distance between serotine colonies (4.1 km ± 0.3 km) and the expected mean distance to the nearest neighbor ($D = \sqrt{\text{colony density}}/2 = 42.7$ km) indicated a non-spatial randomness of colonies and a clear aggregation pattern. Thus, it is legitimate to inquire whether this aggregated distribution is related to the distribution of some habitats.

Thus, we first explored habitat selection by comparisons with random points, finding that serotine bats appear to positively select pastures and areas near streams or water bodies (in both cases $P < 0.01$) while avoiding heterogeneous agricultural areas ($P < 0.001$), which is land principally occupied by agriculture areas with significant areas of natural vegetation, broad-leafed forests ($P < 0.05$), transitional woodland-shrub ($P < 0.05$), and water bodies ($P < 0.01$) (Fig. 2, see also Appendix III). Undeniably, the greatest difference comes from pasture selection (Fig. 2). In addition, serotine roosts are closer to pastures ($\bar{x} \pm SE = 304 \pm 38$ m) and rivers (461 ± 45 m) than are random points (1,096 ± 129 m and 1,054 ± 94 m (in both cases $P < 0.001$). Serotine roosts are also located in areas with greater river density ($P < 0.001$) and higher river confluence density ($P < 0.001$) (greater by a factor of 1.6 and 1.8, respectively — Appendix IV) than random points. However, no significant differences in the distance to nearest wood or forest edge density were detected. In addition, comparison between habitats surrounding serotine roosts with those surrounding random points assessed with Hierarchical partitioning analysis showed that the presence of pastures is the most likely causal factor (Fig. 4). Similar significant results were obtained with pseudo-absence point based on *P. pipistrellus* roosts: for example serotine bats appear to positively select
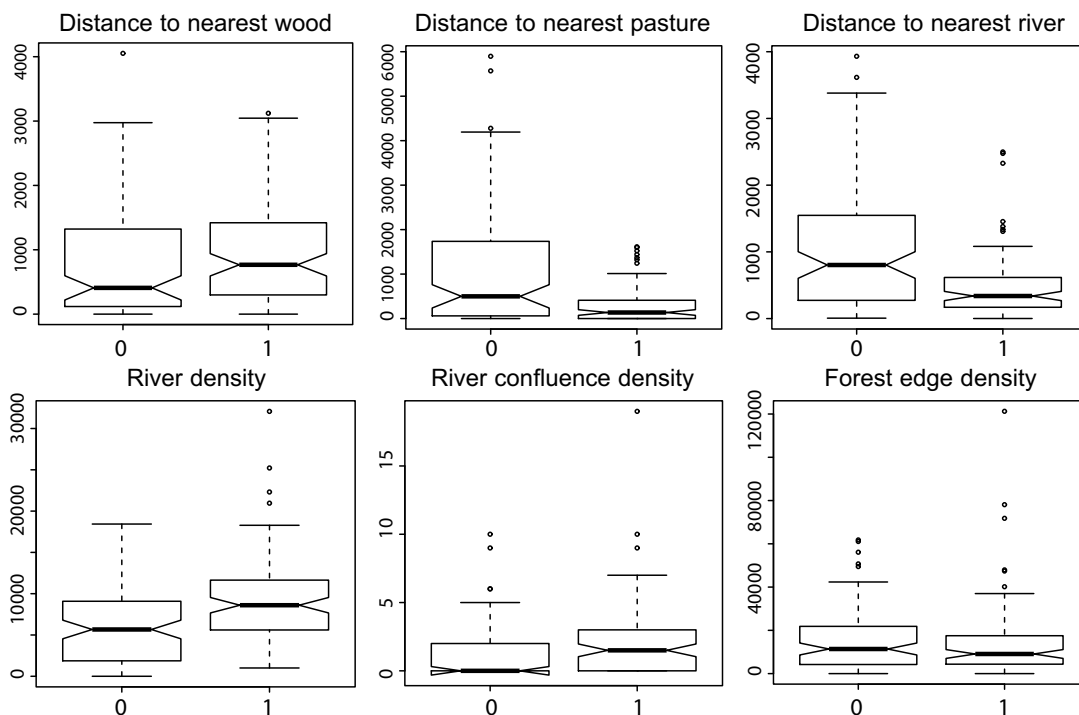

FIG. 3. Boxplot of the differences between serotine bats (1) compared to random points (0) for the selection of the linear elements of landscape or distance to habitat, in a buffer zone of 2,000 m

pastures and areas near streams or water bodies and to avoid heterogeneous agricultural areas and broad-leafed forests. The two main differences are the positive selection of arable land and the avoidance of discontinuous artificial surfaces (Fig. 2).

Hierarchical partitioning analysis for landscape structure showed that the distance to the nearest pasture, the distance to the nearest river and the river density were the most likely causal factors between habitats surrounding serotine roosts compared to random points. With the aim of assessing the joint effects of the major variables of interest and the influence of the size of the buffer, we performed linear models, including simultaneously considering Pasture (H231), Heterogeneous agricultural areas (H242), Land principally occupied by agriculture with significant areas of natural vegetation (H243) and river density as explicative variables. These four variables exhibit no obvious correlation (see Appendix II). We found that serotine bats appear to positively select pastures whatever the scale considered, whereas habitat H243 did not appear as a significant variable whatever the scale considered (Table 1). Habitat H242 and river density appeared to be scale dependent: H242 exhibit a slight trend towards being significant on a small scale, whereas river density appeared only significant at a large scale (Table 1). According to the AIC value, the best model was obtained with a buffer size of 2,000 m.

Effectiveness of this Monitoring in Terms of Serotine Roost Conservation

The sustainability of serotine roosts were negatively influence by changes in facilities carried out by landowners without agreement with the Museum of Bourges (GLM, $\chi^2 = 12.45$, *d.f.* = 1, $P < 0.001$, $\beta = -5.318$), whereas facilities designed by the Museum of Bourges team or in accordance with it did not have a significant effect on the persistence or departure of colonies ($\chi^2 = 0.02$, *d.f.* = 1, $P = 0.88$, $\beta = 0.193$). We did not detect any significant effect of type of facilities ($\chi^2 = 0.42$, *d.f.* = 1, $P = 0.53$, $\beta = -0.294$). In addition, we also detected a significant effect of the year ($\chi^2 = 36.86$, *d.f.* = 22, $P < 0.05$) and the size of the serotine population: larger populations were more stable ($\chi^2 = 16.09$, *d.f.* = 1, $P < 0.001$, $\beta = 1.088$). Finally, we observed that over time, building restorations carried out by landowners without agreement of the Museum of Bourges significantly decreased ($\chi^2 = 7.95$, *d.f.* = 1, $P < 0.01$), whereas we did not detect any trend in the occurrence of building restoration carried out by the Museum of Bourges team or in accordance with it ($\chi^2 = 2.18$, *d.f.* = 1, $P = 0.14$). This suggests that the stronger the link (in terms of year) between the museum and the owner of a building is, the more the likelihood of making arrangements that disrupt colonies decreases.

DISCUSSION

Habitat Selection

This study clearly indicates that even species that are considered generalists (Kerbiriou *et al.*, 2010; Regnery *et al.*, 2013) with regards to the selection of foraging habitat make obvious choices for the location of their breeding colonies. This choice takes the nature of the surrounding habitat into account. Choosing a specific habitat surrounding colonies
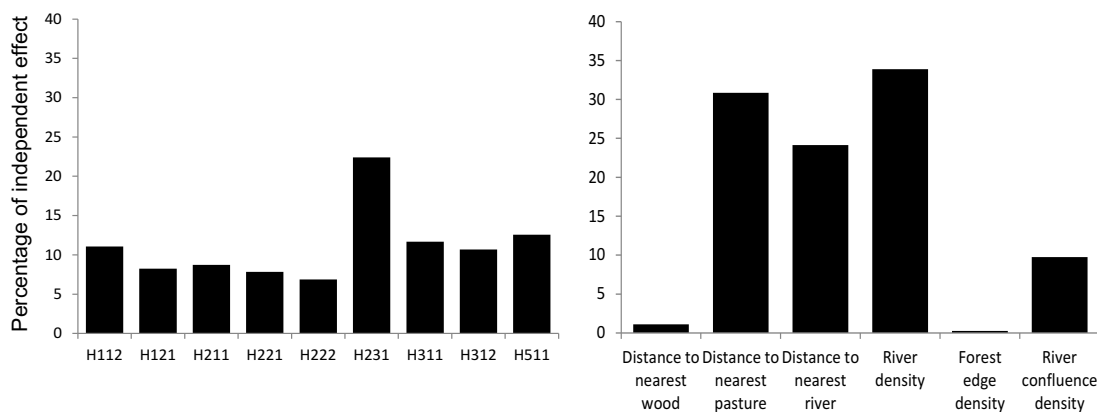

FIG. 4. Identification of the most likely causal factors using hierarchical partitioning. Corine Land Cover habitat typology: H112 — Discontinuous artificial surfaces, H121 — Industrial, commercial and transport units, H211 — Arable land, H221 — Vineyards, H222 — Orchards and berries, H231 — Pastures, H311 — Broad-leaved forest, H312 — Coniferous forest, H511 — Water courses

TABLE 1. Joint effects (*P*-level and AIC values) of the major variables of interest and influence of the size of the buffer in probability of serotine colony presence. Corine Land Cover habitat typology: H231 — Pastures, H242 — Heterogeneous agricultural areas, H243 — Land principally occupied by agriculture, with significant areas of natural vegetation. The model retained based on the smallest AIC value is shown in bold

Buffer size (m)	H231	H242	H243	River density	AIC
100	< 0.05	< 0.05	0.78	0.27	288.8
250	< 0.01	0.09	0.63	0.63	287.2
500	< 0.001	< 0.05	0.54	0.47	276.4
750	< 0.001	< 0.01	0.32	0.46	266.2
1,000	< 0.001	< 0.05	0.66	0.49	261.7
1,250	< 0.001	0.065	0.85	0.40	266.3
1,500	< 0.001	0.081	0.76	0.41	262.1
2,000	**< 0.001**	**0.064**	**0.42**	**0.39**	**255.4**
2,500	< 0.001	0.18	0.89	0.23	263.7
4,000	< 0.01	0.90	0.62	0.05	269.8
6,000	< 0.01	0.94	0.37	< 0.05	269.9
8,000	< 0.01	0.89	0.16	< 0.01	270.5

is even more unexpected for serotine bats, as this species is known to manage quite a long distance between foraging habitats and breeding colonies (11.5 km).

Land use in the Cher region has resulted in a landscape structure in which arable land is negatively correlated with pasture or forest (see Appendix II). Due to this spatial structure, it is possible to directly identify whether serotine bats make a positive selection for one habitat (such as pasture) or avoid another (such as arable land). Our study has identified pastures as the most selected habitat, covering on average 37% of the 2 km buffer around roosts. The majority of studies investigating serotine foraging habitats have made this observation (Catto *et al.*, 1996; Robinson and Stebbings, 1997; Kervyn, 2001). The study carried out by Boughey *et al.* (2011) showed a strong relationship between the probability of *E. serotinus* roosts and the proportion of improved grassland. This affinity to agricultural land is underscored by the proportion of arable land neighboring the roosts (45% on average). However, arable land accounts for the majority of the land use cover of this region; thus, serotine bats appeared to select arable land slightly less frequently than random points. The observed pattern of aquatic habitat selection (% of water stream cover, linear elements) around serotine roosts is in accordance with a large number of studies that have identified the importance of these habitats for *E. serotinus* foraging activities (acoustic studies — Hübner, 1991; Vaughan *et al.*, 1997; Barataud, 1998; Lustrat 2001; Ciechanowski, 2002; Bartonička and Zukal, 2003; Russo and Jones, 2003; Kaňuch *et al.*, 2006; Rainho, 2007; radio-tracking study — Simon *et al.*, 2004; habitats surrounding roosts — Boughey *et al.*, 2011).

A difference between our results and some previous studies (Barataud, 1998; Lustrat, 2001; Russo and Jones, 2003; Rainho, 2007) is the non-selection of forest habitat, particularly broad-leaved woodland. Boughey *et al.* (2011) found a similar result in the UK. Again, it is interesting to consider the habitat surface close (2 km) to serotine roosts: woodland is the third most abundant habitat and covers more than 13% of the area, so a plausible hypothesis is that the current amount of woodland surrounding roosts is sufficient. This possibility explains why we did not detect any selection effect. A second minor difference is the non-selection of urban areas in our study. Due to the selection of roosts in buildings, the proportion of urban areas surrounding serotine roosts is not negligible (6%). However, when comparing this proportion to the proportion of urban areas that surrounded random points, no significant difference could be detected, although some studies have found that foraging serotines choose this habitat (Barataud, 1998; Gaisler *et al.*, 1998; Bartonička and Zukal, 2003; Russo and Jones, 2003; Rainho, 2007).

Conservation Implications

We found that for *E. serotinus*, a species that has a large number of sites available for reproduction because of its ability to use man-made above ground structures, roosts are not distributed randomly. In addition to roost characteristic (not studied here), for their maternity roosts, serotine bats select landscapes with an important proportion of habitats known to be used for foraging (pastoral and aquatic habitats). This result converges with those found by Boughey *et al.* (2011) for *P. pipistrellus*,

P. pygmaeus, *Rhinolophus hipposideros*, *E. sero-tinus* and *Myotis nattereri* sensu lato, that all selected roosts closer to broadleaved woodland than expected by chance. However, the protection of habitats surrounding maternity roosts is not regularly implemented in conservation measures: as an example, in France, most areas dedicated to bat conservation, such as Natura 2000 take into account underground cavities cavities used as roosting sites without taking account the foraging range of the colony or its foraging habitat. Another French regulation called "Arrêté préfectoral de protection de biotope, French law of July 16, 1976", when implemented for bats, only protects the attic or the cavity in which the roost is located and again does not consider the hunting ground associated with the colony. For serotine bats, our results suggest that protection of the foraging habitat around the maternity roost should be considered at least within a radius of 2,000 m. In addition, conservation of this species should focus on pasture maintenance, particularly those close to rivers.

Evaluation of the Proposed Method

The strong convergence of our results with those obtained by radio-tracking or acoustic methods for the identification of the most selected habitats or relevant spatial scale, underlines the robustness of an approach that is based on the spatial distribution of roosts. Moreover, this approach also allows us to study the impact of the landscape structure and clarify some selection processes, such as forest versus forest edges.

The existence of international biodiversity monitoring networks that are based on highly standardized protocols and have a staff of paid experts would be ideal for providing accurate knowledge of species requirements and population trends, among other things (Henry *et al.*, 2008). Therefore, combining the output available from various approaches and ongoing monitoring initiatives is an optimal option. This requires the ability to integrate heterogeneous information on biodiversity, which appears to be more likely due to progress in meta-analysis methodology (Bengtson *et al.*, 2005; Sutherland, 2006; Henry *et al.*, 2008). Thus, analysis of the environment surrounding roosts appears to be a complementary and promising approach for implementing knowledge of the habitat requirements of bats and, especially, for species that have a large number of sites available for reproduction. The species concerned may be those that regularly used

man-made above ground structures, such as *Pipistrellus* spp., *Plecotus* spp., *Rhinolophus ferrumequinum*, *R. hipposideros*, *Barbastella barbastellus*, *Myotis daubentonii* and *M. myotis* (Simon *et al.*, 2004; Dietz *et al.*, 2007; Arthur and Lemaire, 2009; Marnell and Presetnik, 2010). Furthermore, information on roost localization can be accurately gathered by a volunteer network, as in our study. Fortunately, such a volunteer network is also currently being developed in many countries (see Mitchell-Jones *et al.*, 2007; Battersby, 2010; Marnell and Presetnik, 2010; Boughey *et al.*, 2011). Public participation in scientific research is recognized as a promising approach to significantly help scientists address biodiversity issues (Bell *et al.*, 2008; Couvet *et al.*, 2008; Henry *et al.*, 2008). It is likely that the use of data from a study dedicated to the systematic inventory of bat colonies in houses in a relatively large area, such as the Cher (7,300 km², 290 towns and villages, 313,251 inhabitants), by a strictly professional organization would not have generated an unbiased distribution over time and space. If not for limited resources (financial and human), a professional organization would have planned this inventory effort, and the area most likely would have been surveyed sector by sector over time. Thus, the absence of an obvious spatio-temporal bias is likely linked to this volunteer network-based approach. The benefits of volunteer networks are numerous and not only limited to financial savings (Levrel *et al.*, 2010), and these benefits include the fact that citizen monitoring systems are likely to have a high resilience (Couvet *et al.*, 2008), which is the key to maintaining the network over time and thus provide an extended time-series (Battersby, 2010) or large spatial coverage (Jaberg and Guisan, 2001; Lepczyk *et al.*, 2005). In addition, this network provides socially legitimate results that contribute to improving the relevance of results, aid in the identification of key biodiversity issues through discussions between citizens and scientists, and orient public policies and actions towards adaptive management (Couvet *et al.*, 2008).

Finally, such networks involving citizen-landowners have resulted in (i) gathering information from private houses, where access is not easy and authorization demands are highly time consuming; (ii) better monitoring of bat colonies (such observations were noticed by Lepczyk (2005) in a bird survey that integrated citizen science); (iii) increasing the availability of a cost-effective data collection method that provides high quality data that are available for conservation biology investigations and

actions, and (iv) establishing frequent and permanent relationships with the owner, which contributes to securing bat roosts: this relationship significantly decreased the building restoration carried out by landowners without an agreement with the local wildlife rescue networks, as these types of building restorations have been assessed to have a significant impact on the persistence of bat roosts.

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APPENDIX I

Roosts site location of *E. serotinus* (A), *P. pipistrellus* (B) and random points (C) in the Cher region
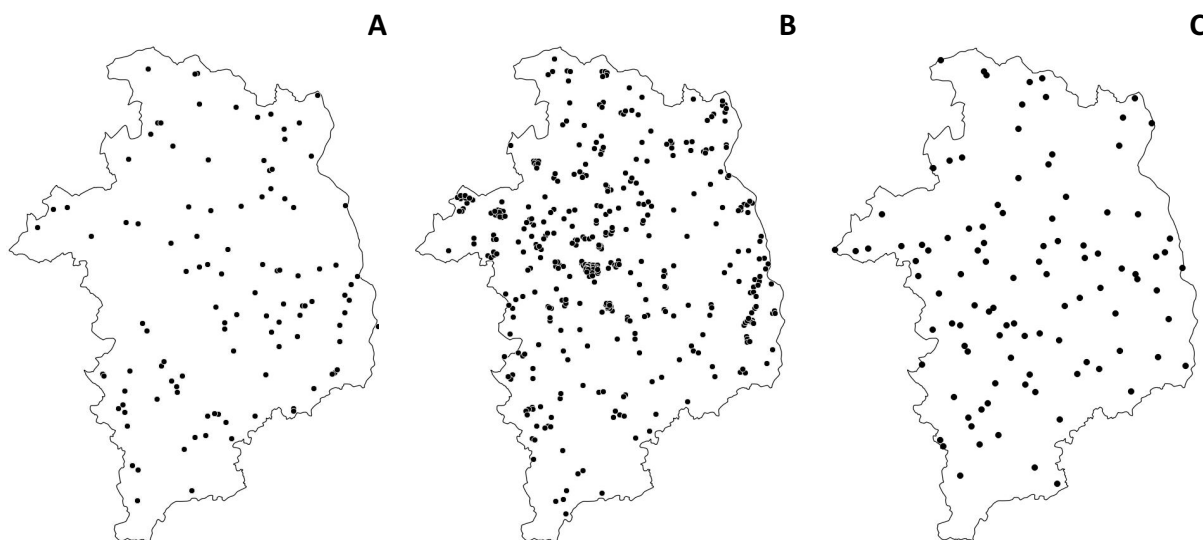
APPENDIX II

Correlations between habitat types (the area of each habitat type within a 2 km² buffer size), as calculated by Spearman's rank correlation. The most important correlations between variables (correlation coefficient $|rho| \geq 0.5$ — see Freckleton, 2002) are indicated in bold. Corine Land Cover habitat typology: H111— Continuous artificial surfaces, H112 — Discontinuous artificial surfaces, H121 — Industrial, commercial and transport units, 131 — Artificial surfaces, dump and construction sites, H211 — Arable land, H221 — Vineyards, H222 — Orchards and berries, H231 — Pastures, H242 — Heterogeneous agricultural areas, H243 — Land principally occupied by agriculture, with significant areas of natural vegetation, H311 — Broad-leaved forest, H312 — Coniferous forest, H313 — Mixed forest, H321 — Natural grasslands, H322 — Scrub and heathland, H324 — Transitional woodland-shrub, H331 — Open spaces with little or no vegetation, H511 — Water courses, H512 — Bodies of water

	H111	H112	H121	H131	H141	H142	H211	H221	H222	H231	H242	H243	H311	H312	H313	H321	H322	H324	H331	H511	H512
H111		0.18	-0.03	-0.01	-0.01	**0.50**	0.04	-0.02	-0.02	0.03	0.03	-0.09	-0.08	-0.03	-0.03	-0.02	-0.01	-0.04	-0.01	-0.02	-0.03
H112			0.41	0.16	0.18	0.33	0.11	-0.05	0.05	-0.08	0.17	0.15	-0.17	-0.01	-0.02	0.03	0.11	-0.18	0.16	0.08	0.02
H121				-0.03	0.37	0.33	-0.12	-0.06	0.18	-0.11	0.08	0.12	0.02	0.01	-0.10	0.14	-0.04	-0.11	-0.03	0.14	0.26
H131					-0.01	-0.02	0.04	-0.02	-0.02	-0.08	-0.10	0.06	0.02	-0.03	-0.03	-0.02	-0.01	-0.04	1.00	**0.51**	-0.03
H141						**0.51**	-0.12	-0.02	-0.02	-0.14	-0.10	-0.09	-0.07	-0.03	-0.03	**0.50**	-0.01	-0.04	-0.01	-0.02	0.27
H142							-0.14	-0.04	-0.04	0.05	0.00	0.00	-0.02	-0.07	-0.07	0.23	-0.03	-0.08	-0.02	-0.04	0.09
H211								0.00	-0.26	**-0.51**	0.11	-0.21	**-0.47**	**-0.46**	-0.19	-0.01	0.09	-0.28	0.04	-0.07	-0.37
H221									-0.04	-0.01	0.09	-0.09	-0.01	-0.07	-0.07	-0.04	-0.03	-0.08	-0.02	-0.04	-0.07
H222										-0.05	0.13	-0.06	0.21	0.32	0.12	-0.04	-0.02	0.09	-0.02	-0.04	0.31
H231											-0.01	0.25	-0.19	0.00	0.00	-0.13	-0.01	0.10	-0.08	0.03	0.16
H242												0.16	-0.16	-0.20	-0.14	-0.14	0.11	-0.20	-0.10	0.10	-0.05
H243													-0.06	0.06	-0.08	-0.02	-0.04	-0.14	0.06	0.25	-0.02
H311														0.38	0.14	-0.06	-0.07	0.27	0.02	-0.09	0.18
H312															0.23	0.09	-0.05	0.14	-0.03	-0.07	0.28
H313																-0.07	-0.05	0.44	-0.03	0.09	-0.01
H321																	-0.03	-0.08	-0.02	-0.04	0.08
H322																		0.17	-0.01	-0.03	-0.05
H324																			-0.04	0.06	0.06
H331																				**0.51**	-0.03
H511																					0.10

APPENDIX III

Differences in the habitat selection of serotine bats compared to random points in a buffer zone of 2,000 m. Corine Land Cover habitat typology: H111 — Continuous artificial surfaces, H112 — Discontinuous artificial surfaces, H121 — Industrial, commercial and transport units, H131 — Artificial surfaces, dump and construction sites, H211 — Arable land, H222 — Orchards and berries, H221 — Vineyards, H231 — Pastures, H242 — Heterogeneous agricultural areas, H243 — Land principally occupied by agriculture, with significant areas of natural vegetation, H311 — Broad-leaved forest, H312 — Coniferous forest, H313 — Mixed forest, H321 — Natural grasslands, H322 — Scrub and heathland, H324 — Transitional woodland-shrub, H331 — Open spaces with little or no vegetation, H511 — Water courses, H512 — Bodies of water. In all cases $d.f. = 1$

Habitat	Estimate ($\beta \pm$ SE)	F-value	P-value
H111	-5.498 ± 14.908	0.14	0.71
H112	-1.466 ± 0.768	3.64	0.06
H121	-1.658 ± 1.502	1.22	0.27
H131	-66.717 ± 94.342	0.78	0.38
H211	-0.395 ± 0.389	1.05	0.31
H221	15.762 ± 17.972	1.22	0.27
H222	-2.947 ± 4.689	0.46	0.50
H231	1.489 ± 0.439	12.56	< 0.001
H242	-68.817 ± 17.953	46.18	< 0.001
H243	-77.409 ± 25.731	41.20	< 0.001
H311	-31.688 ± 20.523	7.61	< 0.01
H312	-0.955 ± 0.567	3.02	0.08
H313	93.656 ± 58.122	7.66	< 0.01
H321	-65.296 ± 55.577	3.79	0.05
H322	-134.422 ± 300.1567	2.48	0.12
H324	-125.700 ± 81.973	10.93	< 0.001
H331	-88.202 ± 141.445	1.25	0.26
H511	-4.193 ± 3.294	4.88	< 0.05
H512	-89.017 ± 45.101	7.87	< 0.01

APPENDIX IV

Differences between serotine bats compared to random points for the selection of the linear elements of landscape or distance to habitat, in a buffer zone of 2,000 m. In all cases $d.f. = 1$

Habitat	Estimate ($\beta \pm$ SE)	F-value	P-value
Distance to nearest wood	0.141 ± 0.062	5.49	< 0.05
Distance to nearest pasture	-0.183 ± 0.053	12.82	< 0.001
Distance to nearest river	-0.498 ± 0.125	19.28	< 0.001
River density	0.741 ± 0.212	38.39	< 0.001
River confluence density	0.820 ± 0.224	14.83	< 0.001
Forest edge density	0.031 ± 0.043	0.72	0.47