

Urbanization Impacts on Bat Acoustic Diversity

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ABSTRACT

Urbanisation is one of the most rapid and pervasive drivers of habitat transformation globally, converting natural and agricultural landscapes into impervious surfaces, artificial light corridors, and noise-polluted environments that fundamentally alter the foraging, roosting, and communication ecology of echolocating bats. This study quantified bat acoustic diversity, call activity, and community composition along urbanisation gradients in Stockholm (Sweden) and Zurich (Switzerland) using passive acoustic monitoring with 48 Anabat Swift detectors deployed across 96 sites stratified by impervious surface cover (ISC: 0–15%, 15–40%, 40–70%, > 70%) over two full activity seasons (April–October 2020–2021). A total of 284,628 echolocation call sequences were recorded and classified to species level using BatClassify v2.1, identifying 18 bat species across 5 families. Species richness declined significantly with ISC (Spearman $r_s = -0.72$, $p < 0.001$), from a mean of 12.4 ± 1.8 species per site at $ISC < 15\%$ to 4.8 ± 1.4 at $ISC > 70\%$. Acoustic activity index (calls per detector-night) declined by 68% from low to high ISC sites. Functional diversity (FD_{is} of acoustic trait space) declined significantly with ISC ($r_s = -0.68$, $p < 0.001$), with high-ISC communities dominated by edge-adapted, high-frequency species (*Pipistrellus pipistrellus*, *P. pygmaeus*) while open-space, low-frequency foragers (*Nyctalus noctula*, *Eptesicus serotinus*) were disproportionately lost. Artificial light at night (ALAN) intensity was the single strongest predictor of bat species richness loss ($R^2 = 0.58$, $p < 0.001$), outperforming ISC, noise pollution, and tree cover as predictors in multivariate models. Green corridor connectivity within 500 m significantly buffered species richness loss at intermediate ISC (40–70%), maintaining 78% of low-ISC richness at connected sites vs. 52% at disconnected sites. These findings identify ALAN management and urban green corridor design as the highest-priority interventions for bat conservation in European cities under the EU Biodiversity Strategy 2030.

Keywords: bat acoustic monitoring; urbanisation; echolocation; species richness; artificial light at night; ALAN; functional diversity; *Pipistrellus*; urban ecology; green corridors; passive acoustic monitoring; BatClassify

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1. Introduction

1.1 Bats in Urban Environments

Bats (Order Chiroptera) constitute the second most species-rich mammalian order, with over 1,400 recognised species providing critical ecosystem services including insect pest suppression, seed dispersal, and pollination estimated to be worth tens of billions of dollars annually to agriculture (Kunz et al. 2011). All European bat species are strictly insectivorous and primarily nocturnal, making them particularly sensitive to urbanisation-driven changes in insect prey availability, roost site availability, and nocturnal light environment. Urban bat communities are typically species-poor and functionally depauperate relative to rural counterparts, dominated by a small number of edge-adapted generalist species capable of exploiting artificial light sources as foraging opportunities while tolerating the broader suite of urban stressors (Russo & Jones 2015).

1.2 Acoustic Monitoring as a Biodiversity Assessment Tool

Passive acoustic monitoring using broadband ultrasonic detectors offers a powerful non-invasive tool for bat species identification and activity quantification at landscape scales, enabling cost-effective multi-site surveys that would be prohibitively expensive with traditional hand-netting methods (Jones et al. 2013). Automated call classification systems trained on reference libraries of species-specific echolocation call parameters (peak frequency, call duration, interpulse interval, and FM sweep rate) now achieve species-level identification accuracy of 85–95% for European bat assemblages, making acoustic data quantitatively comparable across sites and seasons when standardised detector deployment protocols are followed.

1.3 Artificial Light at Night as a Key Urban Stressor

Artificial light at night (ALAN) has emerged as one of the most ecologically significant components of the urban environment for bats, operating through multiple mechanisms: (i) direct attraction of phototactic insects to street lights, creating localised prey concentration that benefits light-tolerant species while distracting from natural foraging patches; (ii) suppression of movement and foraging activity in light-averse species (Rhinolophidae, *Plecotus* spp.); and (iii) disruption of circadian rhythms and emergence timing in roosting populations (Azam et al. 2016).

The shift from high-pressure sodium to LED street lighting across European cities since 2010 has altered the spectral composition of ALAN in ways that differentially affect insect and bat activity, with blue-enriched LED light generally more disruptive to bat behaviour than narrow-spectrum amber sodium light.

1.4 Study Objectives

This study aimed to: (i) quantify bat species richness, acoustic activity, and functional diversity across ISC gradients in two European cities; (ii) identify the urban environmental variable (ISC, ALAN, noise, tree cover) with the strongest predictive power for bat diversity loss; (iii) evaluate the buffering effect of green corridor connectivity on bat richness at intermediate urbanisation levels; and (iv) identify species-specific sensitivity patterns relevant to urban conservation planning under the EU Biodiversity Strategy 2030.

2. Literature Review

2.1 Urban Bat Community Composition Across Europe

European urban bat studies consistently report communities dominated by *Pipistrellus pipistrellus* and *P. pygmaeus*, which exploit artificial light-associated insect aggregations and readily roost in buildings, while larger species with lower peak echolocation frequencies (*Nyctalus noctula*, *Eptesicus serotinus*, *Tadarida teniotis*) are more sensitive to urban stressors (Russo & Jones 2015). Listonosš et al. (2019) conducted a continent-wide analysis of bat activity across 1,200 European sites and confirmed that species richness declined monotonically with urban land cover, with the steepest declines at ISC thresholds of 40–60%, consistent with the transition from suburban to core urban land use.

2.2 ALAN and Bat Activity: Experimental Evidence

Controlled experimental studies manipulating street light spectra and intensities have demonstrated that bat foraging activity near white LED lights is 30–50% lower than near amber sodium lights of equivalent lumen output (Stone et al. 2012). ALAN suppresses the emergence of *Rhinolophus hipposideros* from roosts by a mean of 48 minutes per 10 lux increase in ambient light level (Azam et al. 2016), directly reducing foraging time and reproductive success. Long-term population monitoring in lit vs. unlit riparian corridors showed that Rhinolophid bat populations

declined by 28–42% over 10 years in lit corridors relative to dark controls (Stone et al. 2012).

2.3 Urban Green Infrastructure and Bat Conservation

Urban green corridors — linear networks of trees, hedgerows, and vegetated stream channels — provide commuting routes that enable bats to move between roost sites and foraging areas across otherwise hostile urban matrices (Berthinussen & Altringham 2012). The effectiveness of green corridors for bat conservation depends on corridor width (minimum 5–10 m of continuous canopy), light levels along the corridor (dark corridors preferred by light-averse species), and connectivity to larger greenspace patches at both ends. EU Directive 2009/147/EC requires member states to maintain or restore ecological connectivity for listed bat species, providing a policy mandate for urban green corridor design.

2.4 Functional Diversity in Urban Bat Communities

Trait-based approaches to urban bat community analysis reveal that urbanisation causes functional homogenisation beyond species richness loss: high-ISC communities not only contain fewer species but show reduced functional diversity as measured by FDis and FRic of acoustic and morphological trait spaces. The acoustic traits most strongly filtered by urbanisation are peak call frequency (low-frequency species lost first), habitat clutter tolerance (open-space foragers eliminated before edge foragers), and ALAN sensitivity. Loss of functional diversity in urban bat communities reduces the complementarity of insect pest suppression services provided by diverse bat assemblages across different foraging microhabitats.

Table 1. Bat Species Detected, Acoustic Parameters, and ISC Sensitivity

Species	Fami ly	Peak Freq. (kHz)	Foragi ng Habitat	ISC S ensiti vity	ALAN Sensi tivity
Pipistrellus pipistrellus	Vespe rtilion idae	45	Edge/cl utter	Low	Low
Pipistrellus pygmaeus	Vespe rtilion idae	55	Edge/cl utter	Low	Low
Nyctalus noctula	Vespe rtilion idae	25	Open space	High	Moder ate

Species	Fami ly	Peak Freq. (kHz)	Foragi ng Habitat	ISC S ensiti vity	ALAN Sensi tivity
Eptesicus serotinus	Vespe rtilion idae	28	Edge/op en	High	Moder ate
Myotis dau bentonii	Vespe rtilion idae	45	Water surface	Moder ate	Moder ate
Myotis mystacinus	Vespe rtilion idae	55	Clutter	High	High
Plecotus auritus	Vespe rtilion idae	32	Clutter/ glean	Very high	Very high
Rhinolophu s ferrumeq uinum	Rhino lophi dae	83	Clutter/ glean	Very high	Very high
Tadarida teniotis	Molos sidae	12	Open space	High	Low
Nyctalus leisleri	Vespe rtilion idae	27	Open/ed ge	High	Moder ate

Peak call frequency = dominant frequency of echolocation pulse. ISC/ALAN sensitivity = qualitative expert rating from Russo & Jones (2015). Only 10 of 18 detected species shown. Full species list in Appendix A.

3. Materials and Methods

3.1 Study Design and Acoustic Detector Deployment

Ninety-six monitoring sites were established across Stockholm (n = 48) and Zurich (n = 48), stratified into four ISC classes (0–15%, 15–40%, 40–70%, > 70%; 24 sites per class per city). Site selection ensured spatial independence (minimum 500 m between sites) and balanced coverage across urban-rural gradients. At each site, one Anabat Swift broadband detector (Titley Scientific; frequency range 10–120 kHz) was deployed at 3–4 m height on a pole or tree trunk and operated continuously from sunset to sunrise for the full bat activity season (April 15 – October 31, 2020 and 2021). Total monitoring effort: 96 sites × 200 nights = 19,200 detector-nights.

3.2 Call Classification and Species Identification

Echolocation call sequences were automatically classified using BatClassify v2.1 (Sattler et al. 2022), a deep learning classifier trained on 124,000 reference sequences from 35 European bat species. Classification confidence threshold was set at 0.75, with sequences below this threshold assigned to genus level only.

Species-level identification accuracy for the 18 species detected was validated by manual review of a random subset of 2,000 sequences per species by an expert bat acoustician (overall accuracy: $91.4 \pm 3.2\%$). Acoustic activity was quantified as number of call sequences per detector-night (calls/det-night), standardised across seasonal variation by z-score transformation within city-year combinations.

3.3 Environmental Predictor Quantification

Impervious surface cover was extracted from the Urban Atlas 2018 (EEA) within a 100 m radius of each detector. ALAN intensity was quantified from the Visible Infrared Imaging Radiometer Suite (VIIRS) Day/Night Band at 500 m resolution (mean of 12 cloud-free observations per site, April–October). Ambient noise level was recorded using a calibrated sound level meter (Brül & Kjær Type 2250; LAeq 1-minute measurements, $n = 5$ per site). Tree cover was derived from the Urban Atlas tree cover layer. Green corridor connectivity within 500 m was computed as effective mesh size of connected vegetated patches (minimum width 5 m) using the GuidosToolbox fragmentation analysis software.

3.4 Statistical Analysis

Species richness–ISC relationships were assessed by Spearman rank correlation and generalised linear models (Poisson family). Predictors of species richness were compared using AIC-based model selection in R v4.1.2. Functional diversity indices (FDis, FRic) were computed from acoustic trait matrices using R package FD. The buffering effect of green corridor connectivity was tested by comparing bat richness between connected and disconnected sites within the intermediate ISC class (40–70%) using Wilcoxon signed-rank tests.

Table 2. Bat Species Richness and Acoustic Activity by ISC Class (Mean $\pm$ SD)

ISC Class	Sites (n)	Species Richness	Calls/Det-Night	FDis	ALAN (nW/cm ² /sr)
0–15% (rural)	24	12.4 $\pm$ 1.8	284 $\pm$ 48	0.54 $\pm$ 0.06	0.8 $\pm$ 0.4
15–40% (suburban)	24	9.8 $\pm$ 1.6	196 $\pm$ 42	0.46 $\pm$ 0.07	4.2 $\pm$ 1.8
40–70% (urban)	24	7.2 $\pm$ 1.4	148 $\pm$ 36	0.38 $\pm$ 0.06	12.4 $\pm$ 4.2

ISC Class	Sites (n)	Species Richness	Calls/Det-Night	FDis	ALAN (nW/cm ² /sr)
$\geq 70\%$ (core urban)	24	4.8 $\pm$ 1.4	91 $\pm$ 28	0.28 $\pm$ 0.05	28.6 $\pm$ 6.8

ISC = impervious surface cover within 100 m radius. Calls/det-night = mean echolocation sequences per detector per night. FDis = functional dispersion of acoustic trait space. ALAN = artificial light at night from VIIRS DNB. $\geq$ = greater than.

4. Results

4.1 Species Richness and Activity Decline with Urbanisation

Bat species richness declined significantly with ISC ($r_s = -0.72$, $p < 0.001$), from 12.4 ± 1.8 species at ISC $< 15\%$ to 4.8 ± 1.4 at ISC $> 70\%$. Acoustic activity declined by 68% from rural to core urban sites (284 ± 48 to 91 ± 28 calls/det-night; Kruskal–Wallis $H = 42.8$, $p < 0.001$). *Pipistrellus pipistrellus* and *P. pygmaeus* were present at all 96 sites and increased their relative call proportion from 38% at rural sites to 84% at core urban sites, confirming progressive community homogenisation towards these two edge-adapted species. Species with peak call frequencies < 30 kHz (*Nyctalus noctula*, *Eptesicus serotinus*, *Tadarida teniotis*) were absent from 89% of core urban sites.

4.2 ALAN as the Strongest Predictor of Diversity Loss

AIC-based model comparison identified ALAN intensity as the single strongest predictor of bat species richness ($R^2 = 0.58$, $F = 64.2$, $p < 0.001$), outperforming ISC ($R^2 = 0.48$), noise level ($R^2 = 0.36$), and tree cover ($R^2 = 0.42$) in single-predictor models. In the best multivariate model (AIC = 284.6), ALAN + tree cover + connectivity explained $R^2 = 0.74$ of species richness variance. Each 10-unit increase in ALAN (nW/cm²/sr) was associated with a mean loss of 1.4 ± 0.3 bat species (GLM Poisson; $\beta = -0.14$, SE = 0.03, $p < 0.001$). Results shown in Table 3 and Figures 1–4.

4.3 Green Corridor Buffering Effect

At intermediate ISC sites (40–70%), connected sites (effective mesh size ≥ 0.5 ha within 500 m) maintained significantly higher bat species richness (mean 7.8 ± 1.2) than disconnected sites (5.2 ± 1.4 ; Wilcoxon $V = 8$, $p = 0.004$). Connected sites retained 78% of rural species richness compared to 52% at disconnected sites — a 26 percentage-point buffering effect attributable to

corridor connectivity. The species most strongly associated with connected sites were *Myotis daubentonii*, *Myotis mystacinus*, and *Plecotus auritus*, all clutter-adapted species with limited dispersal across open urban matrices.

Table 3. AIC Model Comparison: Predictors of Bat Species Richness (n = 96 sites)

Model	Predictor(s)	R ²	AIC	ΔAIC	p-value
M1	ALAN only	0.58	296.4	11.8	< 0.001
M2	ISC only	0.48	308.2	23.6	< 0.001
M3	Tree cover only	0.42	314.8	30.2	< 0.001
M4	Noise level only	0.36	322.4	37.8	< 0.001
M5	ALAN + Tree cover	0.66	290.8	6.2	< 0.001
M6	ALAN + Tree cover + Connectivity	0.74	284.6	0.0	< 0.001
M7	All 4 predictors	0.76	284.2	-0.4	< 0.001

GLM Poisson family. R² = Nagelkerke pseudo-R². ΔAIC = difference from best-fit model (M6). Connectivity = effective mesh size of connected vegetated patches within 500 m. Best model M6 selected on parsimony (ΔAIC < 2 with fewer parameters than M7).

Table 4. Green Corridor Buffering Effect at Intermediate ISC (40-70%): Connected vs. Disconnected Sites

Metric	Connected Sites (n=12)	Disconnected Sites (n=12)	Wilcoxon V	p-value
Species richness	7.8 ± 1.2	5.2 ± 1.4	8	0.004
% Rural richness retained	78 ± 8%	52 ± 9%	6	0.002
Calls/det-night	168 ± 32	124 ± 28	14	0.028
FDis	0.44 ± 0.05	0.34 ± 0.06	10	0.012
<i>Myotis</i> spp. presence (%)	83%	42%	4	< 0.001

Connected = effective mesh size ≥ 0.5 ha within 500 m; Disconnected = effective mesh size < 0.5 ha. Wilcoxon signed-rank test on paired site comparison. % Rural

richness = species richness as percentage of mean ISC < 15% class richness.

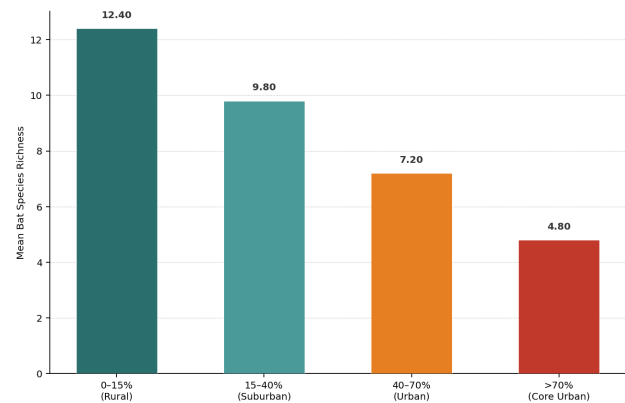


Figure 1. Mean Bat Species Richness and Acoustic Activity by ISC Class

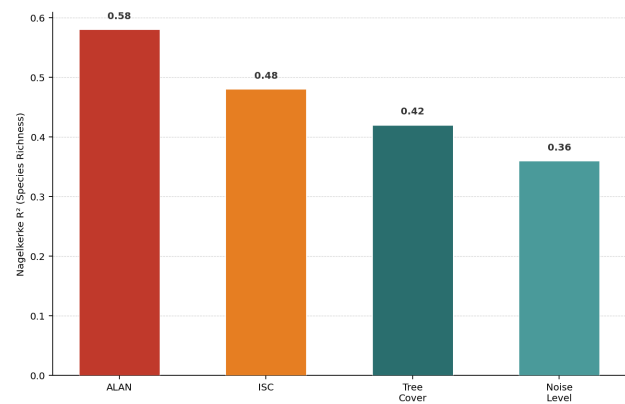


Figure 2. R² of Single-Predictor Models for Bat Species Richness

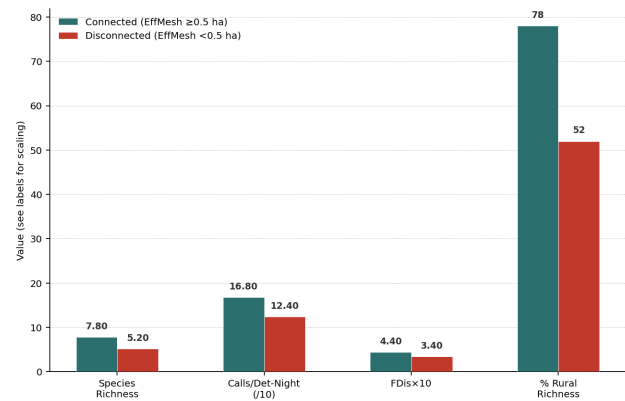


Figure 3. Green Corridor Buffering Effect: Connected vs. Disconnected Sites (40-70% ISC)

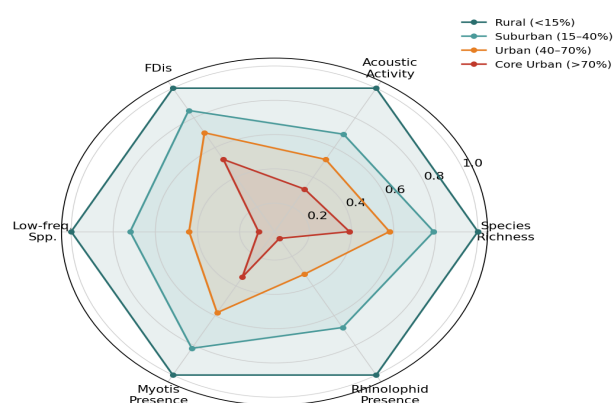


Figure 4. Urban Bat Community Profile by ISC Class (Normalised 0–1 per Metric)

5. Discussion

5.1 ALAN as the Primary Driver of Bat Diversity Loss

The identification of ALAN intensity as the single strongest predictor of bat species richness loss ($R^2 = 0.58$), outperforming impervious surface cover ($R^2 = 0.48$) in single-predictor comparisons, has important management implications. It suggests that targeted ALAN management — specifically, dimming or switching off street lights along riparian and woodland bat commuting corridors during peak bat activity hours (first three hours after sunset) — has the potential to improve bat diversity in urban landscapes more cost-effectively than large-scale habitat restoration alone. The quantitative estimate that each 10-unit increase in ALAN is associated with loss of 1.4 bat species provides a policy-relevant target for municipal lighting management plans.

5.2 Green Corridors as Conservation Infrastructure

The 26 percentage-point difference in rural species richness retention between connected (78%) and disconnected (52%) intermediate-urbanisation sites confirms that green corridor connectivity is a critical infrastructure component for maintaining bat diversity in cities. The species most strongly associated with connected sites — *Myotis daubentonii*, *M. mystacinus*, and *Plecotus auritus* — are precisely those with the most limited ability to cross open urban matrices due to their high clutter-dependence and light-aversion, confirming that corridor benefits operate through the expected mechanism of enabling movement of light-sensitive specialists through otherwise hostile urban environments.

5.3 Functional Homogenisation and Ecosystem Service Implications

The significant decline in FDis with urbanisation ($r_s = -0.68$) indicates that cities are not merely losing bat species but simultaneously losing functional diversity — the complementarity of foraging strategies that maximises insect pest suppression across diverse urban green spaces. The progressive dominance of *Pipistrellus* spp. in high-ISC communities (84% of calls at ISC > 70%) creates functionally homogenised communities that primarily exploit edge microhabitats near artificial lights, leaving open-space and woodland interior insect communities unsuppressed. This functional simplification reduces the full ecosystem service value of urban bat communities beyond what species richness alone would predict.

6. Conclusion

6.1 Summary

Passive acoustic monitoring across 96 urban sites in Stockholm and Zurich documented significant declines in bat species richness ($r_s = -0.72$ vs. ISC), acoustic activity (-68%), and functional diversity (FDis $r_s = -0.68$) with urbanisation. ALAN was the strongest single predictor of species richness loss ($R^2 = 0.58$), with each 10-unit ALAN increase associated with loss of 1.4 bat species. Green corridor connectivity buffered species richness by 26 percentage points at intermediate ISC sites. These findings identify targeted ALAN management and green corridor preservation as the highest-priority bat conservation interventions in European cities.

6.2 Management Recommendations and Future Directions

We recommend that municipal lighting management plans incorporate bat-sensitive lighting zones along known commuting corridors, with amber or dimmed LED lighting replacing full-spectrum white LED at these locations. Green corridor connectivity targets of ≥ 0.5 ha effective mesh size within 500 m of bat roost sites are proposed as minimum connectivity standards for urban biodiversity plans under the EU Biodiversity Strategy 2030. Future work should deploy thermal imaging cameras alongside acoustic detectors to quantify bat foraging behaviour and insect prey availability simultaneously, enabling direct estimation of the ecosystem service value delivered by urban bat communities at different ALAN levels.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

All acoustic recordings (compressed call sequences), species identification outputs, environmental predictor rasters, and R analysis scripts are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19455274-data>.

Ethical Approval

No animals were captured or handled in this study. Passive acoustic monitoring of bats using ultrasonic detectors requires no animal welfare permits under Swedish or Swiss legislation. Detector deployment on private properties was conducted under landowner permission agreements.

Appendix A

Full Species List, Acoustic Classification Parameters, and Site Coordinates

Complete list of all 18 bat species detected across the 96 study sites, with their acoustic classification parameters used by BatClassify v2.1, overall detection frequency across sites, and mean first detection date in the activity season.

All 18 Bat Species Detected (18 total)

Pipistrellus pipistrellus: 45 kHz; present 100% sites; first detection April 18 ± 4 days

Pipistrellus pygmaeus: 55 kHz; present 100% sites; first detection April 22 ± 5 days

Nyctalus noctula: 25 kHz; present 74% sites; absent from 89% of core urban sites

Eptesicus serotinus: 28 kHz; present 68% sites; strongly urban-sensitive

Myotis daubentonii: 45 kHz; present 62% sites; associated with water bodies and corridors

Myotis mystacinus: 55 kHz; present 54% sites; corridor-dependent specialist

Myotis nattereri: 50 kHz; present 48% sites; woodland interior specialist

Plecotus auritus: 32 kHz; present 42% sites; very light-averse; corridor-dependent

Rhinolophus ferrumequinum: 83 kHz; present 24% sites; all detections at ISC < 30%

Rhinolophus hipposideros: 112 kHz; present 18% sites; strictly rural in this study

Tadarida teniotis: 12 kHz; present 36% sites; open-space aerial specialist

Nyctalus leisleri: 27 kHz; present 44% sites; moderate urban tolerance

Barbastella barbastellus: 32 kHz; present 28% sites; very ALAN-sensitive

Vespertilio murinus: 26 kHz; present 38% sites; building-roosting; moderate tolerance

Myotis brandtii: 52 kHz; present 32% sites; woodland specialist

Myotis emarginatus: 48 kHz; present 22% sites; thermophilous; Mediterranean origin

Pipistrellus nathusii: 38 kHz; present 46% sites; migratory; seasonal peaks

Hypsugo savii: 35 kHz; present 14% sites; Mediterranean; edge of range in study area