MASTERARBEIT

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„Habitat use of bats in an urbanised landscape“

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Abstract

All bat species abundant in the Netherlands are protected under the EU's Habitat Directive. In order to ensure the populations' 'favourable state', research on habitat requirements and frequented structures needs to be conducted. Since our landscapes face an increasing trend of urbanisation, the focus lays upon habitats in urban areas.

In 2013 the municipality of Utrecht in cooperation with the Dutch Mammal Society launched a citizen science project to record bat activity throughout the city. The aim was to identify species present within the urban area. We reviewed and analysed the collected data by comparing it to the abundance of habitat structures. Our study reveals the links of species richness and habitat structures as well as species habitat requirements on a temporal and spatial scale.

The species richness and activity highly depends upon the season of recording and increases with a rising number of trees. Further we identified species specific differences in habitat requirements on a spatial and temporal scale.

Zusammenfassung

Alle Fledermausarten, die in den Niederlanden vorkommen, sind unter der europäischen Flora-Fauna-Habitat-Richtlinie geschützt. Studien zur Habitatnutzung sind nötig um den günstigen Erhaltungszustand zu überwachen und zu sichern. Aufgrund des zunehmenden Anteils von urbanen Räumen soll ein Fokus auf Habitaten in Siedlungsgebieten liegen.

Um die Fledermausaktivität im gesamten Stadtgebiet zu erfassen initialisierte die Gemeinde Utrecht zusammen mit der Dutch Mammal Society 2013 ein Projekt unter Mitwirkung von freiwilligen Bürgern der Stadt. Das Ziel des Projektes war es, alle vorkommenden Arten zu identifizieren. Wir haben die Daten mit Bezug zum Vorkommen von Habitatstrukturen im Gebiet bewertet und analysiert. Unsere Studie zeigt sowohl den Zusammenhang von Artenreichtum und Habitatstrukturen auf, als auch die Habitatansprüche der Arten auf einer zeitlichen und räumlichen Skala.

Der Artenreichtum und die Aktivität hängen vom Aufnahmezeitpunkt ab und steigen mit der Anzahl von Bäumen im Gebiet an. Des Weiteren haben wir artspezifische Unterschiede der Habitatansprüche auf einer zeitlichen und räumlichen Skala feststellen können.

Introduction

All bats abundant in Europe are listed in Annex IV of the European Union's Habitat Directory, declaring their need for conservation throughout the member-states (FFH Directory, EU Annex IV: Animal and Plant Species of Community Interest in Need of Strict Protection). The first years after entry into force were devoted to the declaration of conservation areas and identifying areas of conservation interest. Since this process is nearing its completion, interest is now drawn towards species conservation. Annex IV species do not require a conservation area by law, but should rather be protected at any location – including urban areas.

Urban areas have gradually increased in size – and population density – over the last 20 years (HALE ET AL. 2012). In many European states the size of "urban areas exceed those [of areas] protected for conservation" purposes (DEARBORN & KARK 2010). The urbanisation process describes the increasing expansion of urban areas which involves a change of land-use from e.g. landscapes dominated by (semi-)natural habitats to landscapes characterized by an increased level of sealed ground, accompanied by a loss of natural structures and a varying level of disturbance (HALE ET AL. 2012). The remaining green structures often appear as fragmented patches within the concrete matrix. Generally, fragmentation, reduction and transformation of natural habitats threaten global biodiversity. As these factors develop towards extreme intensity in urban areas (AVILA-FLORES & FENTON 2005), one would expect an accordingly low biodiversity. Yet, this issue should be looked at from a local scale, and further should be narrowed down to the requirements of a group of taxa. First, these patches of rather natural habitat may be diverse, ranging from gardens, parks with small woods or large lawns, agricultural land, or linear structures such as channels, hedgerows or tree lined roads. Secondly, for mobile species like bats, patches can represent refuges, or stepping stones for roosts, or provide connectivity between roosts and hunting habitats (OPREA ET AL. 2009). On a macro-habitat scale the heterogeneous structure of an urban area may offer roosting and hunting habitats not available in the homogeneous (agricultural) surrounding environment to some bat species (GEHRT & CHELSVIG 2003, 2004, BIHARI 2004). Assuming a low number of patches and a limited inter-connectivity, preserving those structures is rather important to maintain their functionality (DEARBORN & KARK 2010) and diversity. Additionally the conservation of natural structures within, and along the city's edge may ease the potential adaptation of species to an urban environment (BIHARI 2004, DEARBORN & KARK 2010).

Numerous studies have been conducted regarding the habitat requirements of bats. Lately research on the ecology of bats has included urban environmental aspects more and more frequently (e.g. GAISLER ET AL. 1998, LESINSKI ET AL. 2000, LEGAKIS ET AL. 2000, BARTONICKA & ZUKAL 2003, SACHTELEBEN & VON HELVERSEN 2006, STOYCHEVA ET AL. 2009, KUBISTA 2009, PEARCE & WALTERS 2012, HALE ET AL. 2012, LE ROUX & LE ROUX 2012, DUARTE 2013, MASING 1999, 2013). Many studies have been conducted focussing on either, single species and their requirements (in urban or natural habitat), or on particular factors potentially affecting bat activity, e.g. light pollution or distance to woods (e.g. RYDELL 1992, OPREA ET AL. 2009, LEWANZIK & VOIGT 2013). Living in a world where urban areas are expanding gradually, and with the European law regulating negative effects on species and habitats of conservation interest, the research on urban ecology aspects is gaining importance.

As bat species' "favourable state" needs to be preserved by law, the knowledge of potential habitat use in the urban environment is fundamental for an ecologically sustainable city development aiming to make urban areas more accessible for wildlife. The Netherlands is a highly urbanized country where 89% of its total population live in urban areas (http://data.worldbank.org/indicator/SP.URB.TOTL.IN.ZS). In rural areas bat populations have been rather well mapped and studied by monitoring projects of the Dutch Mammal Society (JANSEN ET AL. 2012, LIMPENS 2012, LIMPENS & JANSEN 2013, HOLLANDER ET AL. 2013, JANSEN & LIMPENS 2014), but since many species may be encountered even in the city centre their habitat needs to be researched. This study will evaluate habitat variables potentially affecting the activity of bats. It aims to show the habitat needs of occurring bat species.

In general green structures within an urban area are important to support bat diversity, even though some species have adapted to a life in urbanised areas. It is widely agreed the availability of water and vegetation is existential. The neighbourhoods with large parks and a lower density of buildings, situated in the outskirts of a city, are especially favoured by bats and show a higher species richness (LEGAKIS ET AL. 2000, AVILA-FLORES & FENTON 2005, KUBISTA 2009, OPREA ET AL. 2009, OBRIST ET AL. 2012). The presence of wooded areas is positively related to species richness and bat activity (GEHRT & CHELSVIG 2003, MEHR ET AL. 2010). Furthermore VERBOOM & HUITEMA (1997) point out the importance of meadows and grasslands as foraging habitats for *Eptesicus serotinus*, a species hunting rather large beetles related to crops. Smaller species like *Pipistrellus pipistrellus* tend to avoid open areas and use structural elements like trees and hedges as wind shields. DAVIES ET AL. (2012) refer to the importance of gardens as heterogeneous habitat patches for *P. pipistrellus*. Gardens may play a vital role in making urban areas accessible for bat species as they provide small-scale and diverse structures that fulfil various functions of foraging, roosting and flyway habitats.

Additionally the availability of waterbodies whether as foraging habitat or linear structure guiding flightpaths, is considered a necessity to present bats (ENTWISTLE ET AL. 1997, MEHR ET AL. 2010). However, in urban areas the effect of bats drawn to water is less intense due to the enhanced availability of water compared to rural (agricultural) areas. Besides an overall positive effect of these green structures on bat activity and species richness, we expect to discover species specific patterns of habitat use.

Species roosting in built structures, e.g. *P. pipistrellus* and *E. serotinus* (CATTO ET AL. 1996, JONES & ALTRINGHAM 1996, TEIGE 2009, LESINSKI ET AL. 2013, ARTHUR ET AL. 2014), are more abundant in urban areas than tree dwelling species (OPREA ET AL. 2009). Since *P. pipistrellus* roost in buildings, fly along linear structures, and may also hunt around streetlamps, it is the most common urban bat species (DIETZ ET AL. 2007, STOYCHEVA ET AL. 2009). However tree roosting species such as *Nyctalus noctula* and *Pipistrellus nathusii* are commonly found throughout cities in central Europe (LUNDY ET AL. 2010, KUSCH & SCHMITZ 2013, MASING 2013). The availability of buildings is driven by the architecture – access to cavities and climate. Within urban areas we observe a gradient concerning building density, disturbance, noise and green structures from the centre towards the edge (AVILA-FLORES & FENTON 2005). Whether noise impacts bat presence in urban areas is debated and has not yet been researched in depth. For Athens LEGAKIS ET AL. (2000) found an avoidance of suitable hunting habitats with a high noise level, while BIHARI & BAKOS (2001) discover no influence of noise on the choice of roosting sites.

Various studies have been conducted regarding the effect of artificial light on nocturnal animals like bats (RYDELL 1992, PATRIARCA & DEBERNARDI 2010, OBRIST ET AL. 2012, LEWANZIK & VOIGT 2013). The main concern lays in the suitability of an illuminated environment for nocturnal animals, which depends on the quality of light source. Yet, some rather fast flying species with long range echolocation systems forage under streetlamps (RYDELL 1992, AVILA-FLORES 2005, LEWANZIK 2013). They benefit from high insect abundance around those artificial light sources, where energy intake may be many times higher than in natural hunting areas. *P. pipistrellus, N. noctula, Vespertilio murinus* and *P. nathusii* are considered species that exploit insect accumulations at streetlights (RYDELL 1992, DIETZ ET AL. 2007). PATRIARCA & DEBERNARDI (2010) were led to the hypothesis that *P. pipistrellus'* expanding occurrence throughout Switzerland may be due to their ability to exploit artificial light sources. However, even these rather tolerant species avoid roost sites in bright environments (LEWANZIK & VOIGT 2013). It should be highlighted that the advantage of streetlamps is restricted to the foraging of a few species. Many other species with high conservation interest, e.g. *Myotis* and

Rhinolophus species, do not benefit from light sources and are excluded from this hunting privilege (LEWANZIK & VOIGT 2013).

One would however expect that a higher amount of green structures, especially wooded areas, does increase the presence and activity of bats. While urban indicators, such as high density of built areas, sealed ground and traffic noise, might have a negative effect on bat activity. The existence of a minimum of green structure influences the roost selection positively, thus the combination of green and urban structures gives an idea of appropriate habitat (KUBISTA 2009).

Further we want to find out whether all parameters we expect to influence bats actually do affect their presence. The presence and activity of bat species within the city have been surveyed. Taking the mobility of bats and their annual cycle into account, this study aims at answering whether there are differences in habitat requirements on a spatial and on a temporal scale.

Urban areas are usually rich in species, though most are generalists and adapt easily to a changing environment. Here, species richness, species composition and the occurrence of individual species across an urbanisation gradient are used as indicator measures to study the response of bats to our increasingly urbanised landscape.

Methods

Study area

Utrecht, with more than 320.000 inhabitants, is the Netherland's fourth biggest city. It is located near the capital Amsterdam, and rather central within the country. The city is surrounded by the Dutch Polder landscape which is characterised by extensive grasslands and fields crossed (and drained) by many narrow channels. Greater forests are situated towards the east, but the extensions of the *Utrechtse Heuvelrug* National Park do not reach the city's borders. Hence, the study area, restricted to the city's boundaries, only includes small fragments of woods along the outskirts or within its parks. Utrecht is characterised by a number of channels of varying sizes, many lined by trees or other green structures. Along the western side flows the river *Vecht*. The very centre of the city is rather compact. As Utrecht is an important transportation hub, it is surrounded by motorways and divided by the railway system. Buildings in the central housing areas are traditionally brick houses with 2-3 floors, while the outskirts are dominated by new housing estates with modern family homes. Throughout the city high buildings with more than 6 floors are scarce. Many old churches, a few windmills and water-towers of the city may offer roosting sites for bat species roosting in buildings.

Selection of study sites

This study is based on a project of the municipality of Utrecht. It was set up in 2013 in cooperation with the Dutch Mammal Society (Zoogdiervereniging) in order to survey bat activity within the city. Data was gathered by a working group of volunteers in their private grounds, hence the study sites are randomly spread across the city. They represent an urbanisation gradient from the far outskirts to the very city centre. Because study sites were exclusively on private land, the industrial areas and city parks could not be considered within this study. A total of 73 locations were selected for bat surveys using two bat recorders (Fig. 1).

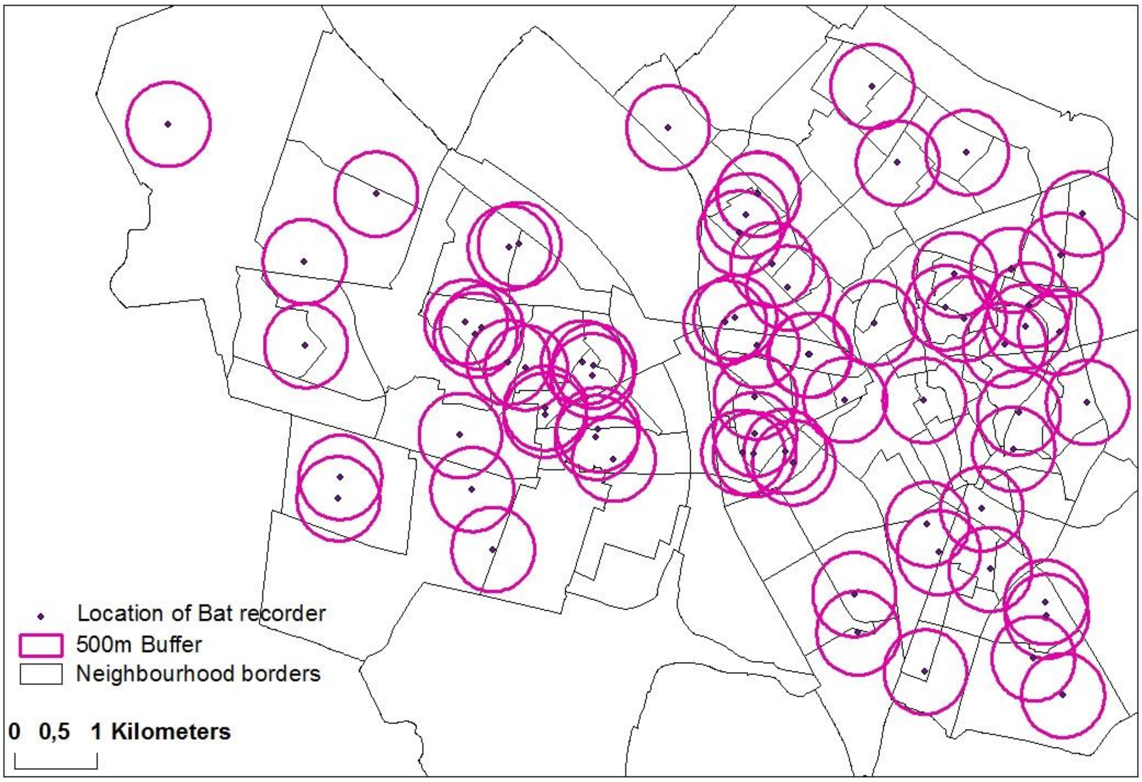

Figure 1 Location of study sites with 500m radius in Utrecht

Recording of Bat activity

At each study location echolocation calls were recorded with a batlogger (*Elekon AG*) and subsequently have been analysed by the *Zoogdiervereniging* with the aid of *Batscope* software. The recording frequency was defined for 12 seconds with an automatic filter for more than 400 recordings in one night. All passages were aggregated per night (JANSEN & HOLLANDER 2014). Since this study aims at identifying overall habitat use no distinction between social, foraging and orientation calls was made. Naturally activity levels are higher around roosts and foraging sites. By recording echolocation calls it is impossible to calculate species abundance, though LINTOTT ET AL. (2013) state that for *P. pipistrellus* the activity levels correlate with abundance.

The recording of bat activity was carried out between 15th April and 30th October 2013. Both *batloggers* were exchanged infrequently between the study sites. Therefore the number of recording nights varies from one up to 14 with a mean of 2.9 nights at each location (75.3% were surveyed 2-4 nights, 16.4% one night and 8.2% >5 nights). As activity was recorded at different times throughout the year, we have to incorporate this factor into our analysis. Adding the temporal scale is important as bats follow an annual cycle of, simplified, mating season in autumn, hibernation in winter, pregnancy in spring and maternity during summer. Each phase takes place in different habitats, with migration and temporary roosts in between. Times and factors are species specific. Since habitat use of bats can differ in the course of their reproductive cycle, the survey nights were separated into three periods. A mean activity was calculated for each period. As most locations were only surveyed in one period, for those studied in several, one was randomly chosen. The recording time does not include winter leaving three significant periods in the bat's reproductive cycle. Period A labels the phase of pregnancy, stretching over 6-8 weeks during May-June (DIETZ ET AL. 2007). Some females start as early as April to settle in maternity roosts, depending on weather conditions and species. Male bats start to frequent their summer roosts. During period B, spanning from July to August, reproductive females nurse their offspring. In many species roosting sites stay the same for period A and B. The differentiation is chosen due to variation in foraging. From September maternity roosts are abandoned and mating season begins. Some species are stationary while others migrate to their hibernation areas. This phase was recorded in September and October as period C (BAGGOE 2001, BERG & WACHLIN 2004A, 2004B, DAVIDSON-WATTS ET AL. 2006, KAPFER & ARON 2007, GELHAUS & ZAHN 2010, PLANK ET AL. 2012, LÓPEZ-ROIG & SERRA-COBO 2014, HARGREAVES ET AL. 2015).

Habitat variables

To identify habitat requirements and gain knowledge on species richness we mapped the study sites, identified environmental structures, and related their abundance to the recorded bat activity. To compare habitat requirements on varying spatial scales we drew buffer zones around the *batlogger*'s exact location with different radii of r=100m, r=250m and r=500m (Fig. 2). For the mapping process we combined data provided by the municipality of Utrecht, *Google Earth* (2007) and field observations (June-July 2014) in *ArcGIS 10.1 (ESRI)*. In total 10 variables, which could potentially affect habitat quality for bats, were measured. Most of the environmental structures were measured regarding the area they cover. The percentages of cover were extracted for these variables. Some, however, were quantified by the total number of elements or categorical.

The variables “buildings” and “sealed ground” can be used as direct measurements for the extent of urbanisation. “Buildings” quantifies the area covered by any house-like structure from garden huts, churches and office buildings to ordinary housing areas. The noise-level, mainly created by traffic and industry, and the density of streetlamps are additional indicators for urbanised areas. Both variables are based on data derived from the municipality of Utrecht. “Number of streetlamps” contains the total number of lampposts within a bufferzone. Data on noise-level was provided as minimum and maximum value, both generated as categories spanning over 5dB each. For our analysis we chose the category's lower limit for minimum value (30 - 45dB) and the upper limit for maximum value respectively (45 - ≥80dB).

The parameters describing green structures within the city are mostly joint categories of rather natural structures and similar man-made structures. "Private land" comprises rather urban green areas since it describes heterogeneous small-sized structures like grave yards, some sports grounds, but mainly private gardens. Therefore this variable describes a small scale composition of the following green structures, which in this case due to size and heterogeneity may be merged into one category.

We divided these green structures into two spatially measured categories: "open land" and "wooded areas". "Open land" includes lawns, meadows, pastures and fields. It may include extensive grasslands as well as agricultural fields, the latter being scarce within the city's boundaries (compare Fig. 2). The variable "wooded area" contains woodlots, small woods in parks, hedges, orchards and tree nurseries.

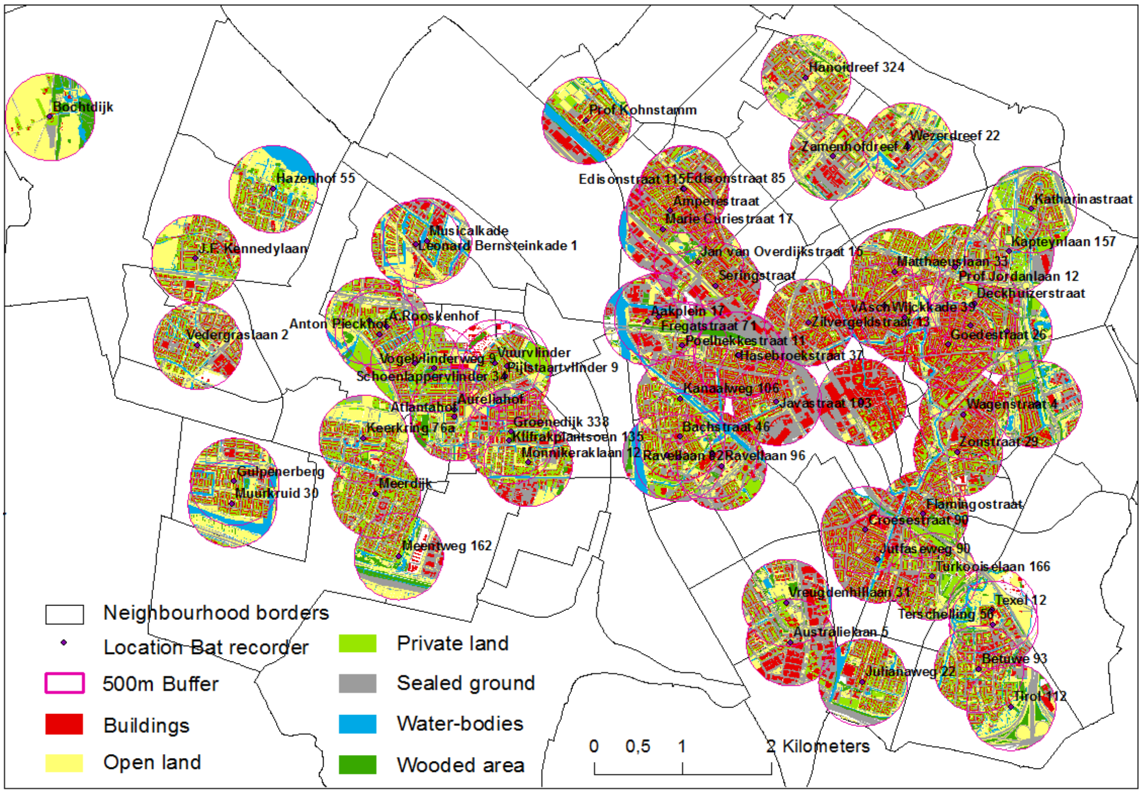

Figure 2 Study sites with environmental structures mapped for 500m buffer

Any tree may offer roosting sites for tree dwelling bats but it also certainly provides foraging opportunities. Therefore the "number of trees" was established as a separate parameter, as well as the category of "potential roosting trees" known for either cavities or bat boxes. Both variables are measured in total numbers. Further the cover of “water-bodies”, including lentic and lotic systems, was quantified.

The statistical analysis will be conducted with the following ten variables:

I Buildings

II Sealed ground

III Private land

IV Open land

V Wooded area

VI Water-bodies

VII Number of streetlamps

VIII Number of trees

IX Number of potential roosting sites

X Noise

Data analysis

We extracted the values of the ten variables for all buffer zones from *ArcGIS 10.1*. To achieve normality of the variable’s values square-root-transformation was conducted accordingly. We obtained one file for each bufferzone, containing environmental variables. Values of all environmental variables were standardised prior to all conducted statistical analyses.

As the number of recording nights varied by location, we calculated the mean night activity for each period. Hence, species data was filed as mean activity per study site and recording period. Data was only considered for further analyses when sufficient (≥5 recordings) for one or more periods. Thus *Myotis mystacinus, M. dasycneme* and *Plecotus auritus* were only included in analyses referring to presence-absence data. We acquired three data sets, one per period, containing the mean activity data of species sufficiently recorded. All statistical analyses were calculated either with *IBM SPSS statistics 22* or *Statsoft Statistica 10*.

We used Spearman-Rank-Correlation to relate species activity to environmental variables and performed the Mann-Whitney U-test to test for differences between study sites with and without recorded activity. The results of both tests led to a pre-selection of significant variables for multivariate analysis (see Appendix Tables 1 and 2). Hereby we excluded the variables “sealed area” and “max. noise” from analysis regarding species specific habitat use. Further, we did not use data obtained for the buffer zone of r=500m to avoid spatial autocorrelation due to the high extent of overlap of resulting circles around study sites.

To evaluate the importance of landscape variables for species richness we used a model selection following an information-theoretic approach (BURNHAM & ANDERSON 2002). Calculated models included all possible combinations of landscape variables and were subsequently ranked using the Akaike Information Criterion corrected for small sample size (AICc). We then checked for correlations of variables with other variables (see Appendix Table 3) and decided not to include “open area” and “sealed ground” in further analyses referring to species richness. “Period” was considered as a variable for species richness. For all calculated generalized linear models we used a Poisson error distribution and a log-link function.

A presence-absence data set was prepared for all 10 species. We tested for nestedness of recorded species assemblages using *Nestcalc* and *Aninhado* (GUIMARÃES & GUIMARÃES 2006).

To identify the influence of environmental variables on species activity we created simple canonical correspondence analysis (CCA) plots with *Canoco 4.5* and *CanoDraw* (TER BRAAK 1986). In order to compare the variables in their importance to species in different seasons, plots were generated for each period. For the comparison between different spatial scales, plots were calculated separately for the 100m and 250m buffer zones.

Results

Species richness

In total the activity of ten species was recorded, of which seven provided sufficient data sets for at least one period (*P. pipistrellus, P. nathusii, P. pygmaeus, N. noctula, E.*

Figure 3 Species numbers at study sites

serotinus, V. murinus, M. daubentonii). *P. pipistrellus* occurred at all 73 study sites. The number of recorded bats varied between one and eight species per site. The mean number of recorded species per site (± SD) was 3.29 (±1.65). Locations with a high number of species are located within the city centre as well as in the suburbs (Fig. 3). A clear spatial pattern along a gradient from the centre to outskirts cannot be observed. Locations with activity of *Myotis spp*. are situated along the city's borders.

Table 1 Best models (ranked according to their AICc) evaluating the importance of habitat variables within a 100 m buffer around survey points for bat species richness. (A) Model parameters: number of included parameters (K), Akaike's Information Criterion corrected for small-sample size (AICc), difference between model's AICc compared with the lowest AICc of the best model (Δ AICc), and the AICc weights (wi). (B) Model coefficients and standard errors (in brackets) are provided for all parameters included in the respective models.

		Model ranking						
		1.	2.	3.	4.	5.	6.	7.
(A) Model parameters								
K		3	2	4	4	3	4	4
AICc		219.71	220.76	220.93	221.10	221.28	221.35	221.47
Δ AICc		0.00	1.05	1.22	1.39	1.57	1.64	1.75
w_i		0.05	0.03	0.02	0.02	0.02	0.02	0.02
% deviance explained		53.28	56.5	52.26	52.43	54.85	52.68	52.79
(B) Included variables								
Intercept		0.88 (0.14)	0.92 (0.13)	0.87 (0.14)	0.87 (0.14)	0.90 (0.14)	0.87 (0.14)	0.89 (0.14)
Period	A	0.25 (0.18)	0.20 (0.18)	0.26 (0.18)	0.24 (0.18)	0.22 (0.18)	0.26 (0.18)	0.22 (0.18)
	B	0.55 (0.17)	0.51 (0.16)	0.55 (0.17)	0.58 (0.17)	0.51 (0.16)	0.54 (0.17)	0.54 (0.17)
	C	0[a]	0[a]	0[a]	0[a]	0[a]	0[a]	0[a]
Trees		0.12 (0.07)	–	0.12 (0.06)	0.12 (0.07)	–	0.10 (0.07)	0.11 (0.07)
Roost trees		–	–	-0.07 (0.07)	–	–	–	–
Water bodies		–	–	–	-0.06 (0.07)	–	–	–
Wooded area		–	–	–	–	0.08 (0.06)	0.05 (0.07)	–
Streetlamps		–	–	–	–	–	–	0.05 (0.06)
Private land		–	–	–	–	–	–	–
Noise min.		–	–	–	–	–	–	–
Buildings		–	–	–	–	–	–	–

[a] coefficients are redundant, hence they are set to zero

Table 2 Best models (ranked according to their AICc) evaluating the importance of habitat variables within a 250 m buffer around survey points for bat species richness. (A) Model parameters: number of included parameters (K), Akaike's Information Criterion corrected for small-sample size (AICc), difference between model's AICc compared with the lowest AICc of the best model (Δ AICc), and the AICc weights (wi). (B) Model coefficients and standard errors (in brackets) are provided for all parameters included in the respective models.

		Model ranking					
		1.	2.	3.	4.	5.	6.
(a) Model parameters							
k		3	4	4	4	4	4
AICc		218.65	220.09	220.20	220.22	220.43	220.49
Δ AICc		0.00	1.65	1.76	1.78	1.81	1.99
AICc weight		0.07	0.03	0.03	0.03	0.03	0.03
% deviance explained		52.51	51.93	52.03	52.06	52.27	52.33
(b) Included variables							
Intercept		0.89 (0.14)	0.89 (0.14)	0.89 (0.13)	0.89 (0.14)	0.89 (0.14)	0.90 (0.14)
Period	A	0.25 (0.18)	0.26 (0.18)	0.24 (0.18)	0.25 (0.18)	0.24 (0.18)	0.24 (0.18)
	B	0.49 (0.16)	0.48 (0.17)	0.50 (0.17)	0.50 (0.17)	0.50 (0.17)	0.49 (0.16)
	C	0[a]	0[a]	0[a]	0[a]	0[a]	0[a]
Trees		0.13 (0.06)	0.12 (0.06)	0.13 (0.06)	0.14 (0.07)	0.13 (0.06)	0.12 (0.07)
Roost trees		–	–	–	–	–	–
Water bodies		–	–	-0.05 (0.07)	–	–	–
Wooded area		–	–	–	-0.05 (0.07)	–	–
Streetlamps		–	–	–	–	–	0.03 (0.06)
Private land		–	-0.05 (0.07)	–	–	–	–
Noise min.		–	–	–	–	-0.03 (0.07)	–
Buildings		–	–	–	–	–	–

[a] coefficients are redundant, hence they are set to zero

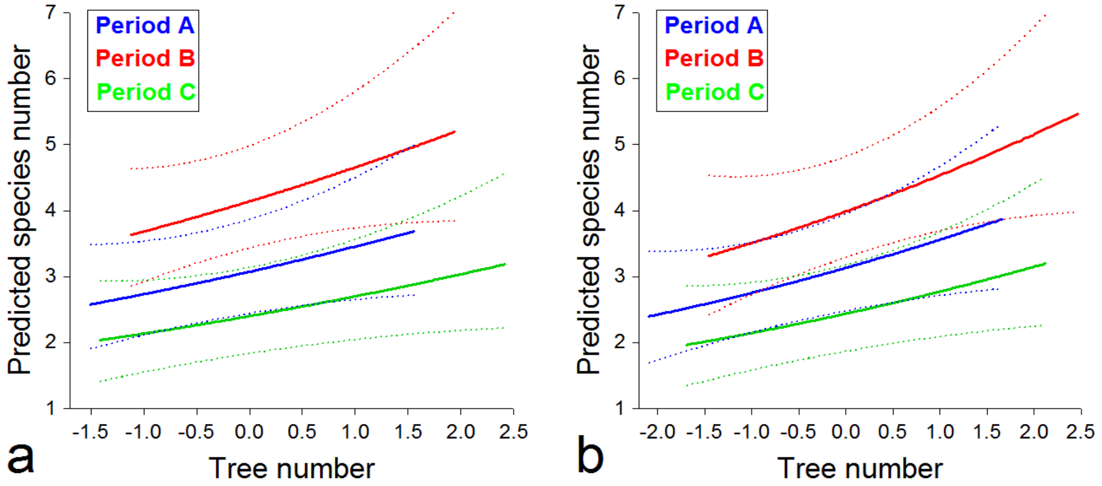

Figure 3 Relationship between species numbers and the number of trees within (a) a 100 m buffer and (b) a 250 m buffer around survey points as predicted by the best GLMs evaluating effects of various environmental variables on bat species richness (compare Table 1 and 2)

Nestedness of bat assemblages

When considering data of all survey periods, the recorded bat assemblages proved to be highly nested (Fig. 5). The average system temperature (± SD) for 100 randomly generated matrices of 57.09° (±4.98°) deviated significantly from the temperature of the packed matrix based on our actual data (pP(T<2.2°) < 0.0001). Similar results (not shown) indicating highly nested species assemblages were obtained when our data were analysed separately for the three survey periods A-C.

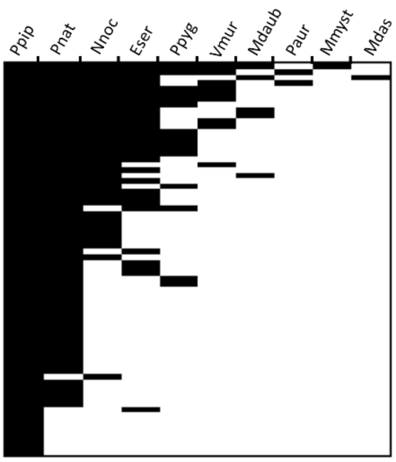

Figure 5 Presence-absence matrix of bat species recorded at 73 study sites packed into the state of maximum nestedness. Study sites are in rows, bat species are in columns. Bat species: Ppip – *Pipistrellus pipistrellus*, Pnat – *Pipistrellus nathusii*, Nnoc – *Nyctalus noctula*, Eser – *Eptesicus serotinus*, Ppyg – *Pipistrellus pygmaeus*, Vmur – *Vespertilio murinus*, Mdaub – *Myotis daubentonii*, Paur – *Plecotus auritus*, Mmyst – *Myotis mystacinus*, Mdas – *Myotis dasycneme*

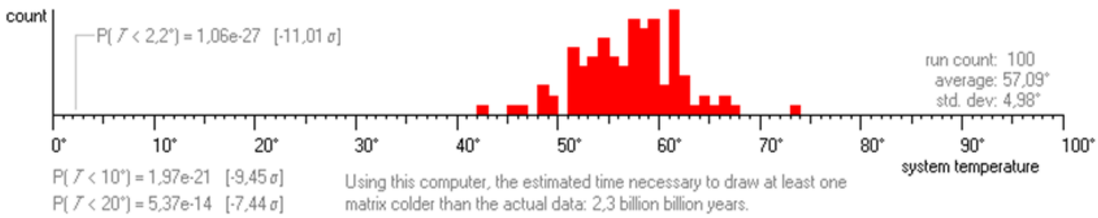

Figure 6 Calculated system temperature with a runtime of 100 for all periods

Species habitat requirements

Pre-selection of environmental variables by applying Spearman-Rank-Correlations and Mann-Whitney U-tests (Tab. 3) eliminated “sealed area” and “max. noise”, leaving nine parameters to be analysed on their importance for bat species. Though “number of streetlamps” and “min. noise” do not correlate with the species data for the 100m and 250m buffers, they were incorporated in multivariate analysis since they proved to be important explanatory variables in other studies analysing effects of urbanisation on various animal species.

For *N. noctula* and *E. serotinus* we discovered correlations between activity with green structures like woods and trees, furthermore private and open land correlates with the activity of *N. noctula. V. murinus*’ activity was related to buildings on both spatial scales.

Overall the variables “open land”, “number of trees” and “buildings” show the highest importance for bat activity (see also Appendix Tables 1-2).

Table 3 Number of significant results of Spearman-Rank-Correlation and Mann-Whitney U-Test, testing relationships between activity of individual bat species and 10 different environmental variables in 100m and 250m buffers

	Sealed area	Buildings	Street-lamps	Noise min	Noise max	Private land	Wooded area	Trees	Open land	Water-bodies
100m	0	2	0	0	0	1	2	1	2	1
250m	0	1	0	0	0	1	0	2	2	0
SUM	0	3	0	0	0	2	2	3	4	1

Species habitat requirements on a spatial scale

On a spatial scale we first take a look at environmental parameters predicting species activity in the established buffer zones not considering season. Firstly, it is highly noticeable that *P. pipistrellus* occurred on both spatial scales right in the centres of the CCA plots indicating that it is the most tolerant species of those considered (Fig. 7 and 8). On a small scale approach the parameters open land, waterbodies, wooded area, private land and number of trees represent the main factors related to the activity of individual species, while buildings, minimum noise and the number of streetlamps do not factor in much (Fig. 7). On a larger scale the variable open land gains in influence (Fig. 8). Most species are plotted close to the vector number of trees.

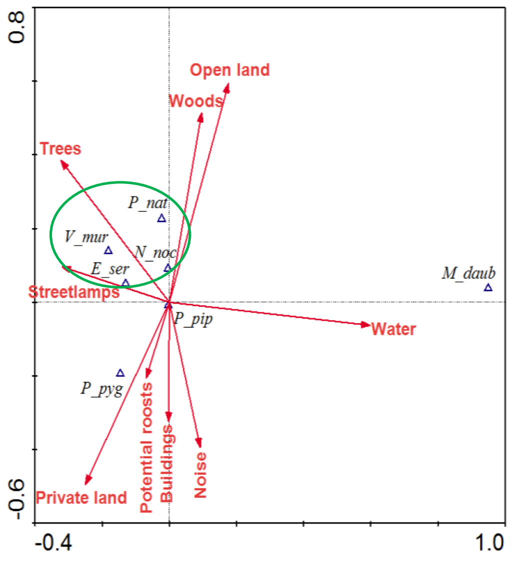

Figure 7 Environmental Parameters predicting species activity in 100m Buffer

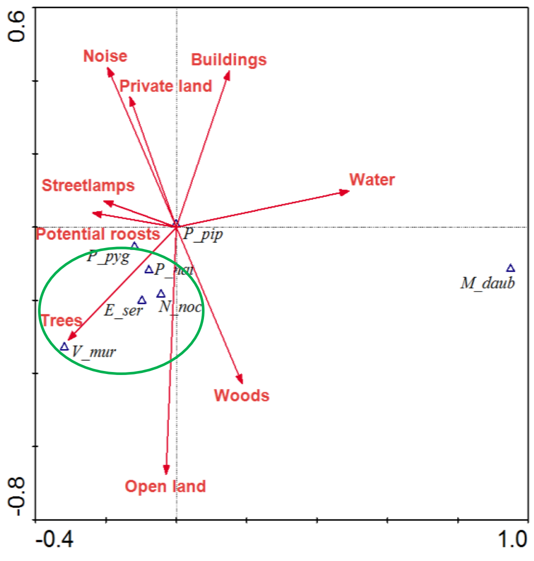

Figure 8 Environmental Parameters predicting species activity in 250m Buffer

Looking at the species separately, we see no differences in structural requirements on a spatial scale for *M. daubentonii*, which on both levels shows a significantly different use of habitat structures from all other species. Of the investigated species it is the least tolerant towards the environmental parameters. Water plays a significant role in modelling its habitat, while variables typical for urban areas such as the number of streetlamps and gardens are avoided.

The remaining species seem rather tolerant towards the analysed habitat structures. *N. noctula, P. nathusii* and *V. murinus* tend to be drawn towards green structures like open land or woods. For the two latter we notice the requirement of trees. At least on a smaller scale *P. pygmaeus* and *E. serotinus* correlate with urban parameters such as streetlamps and gardens.

Looking at differences in spatial scale including the recording time as a co-variable, *P. pipistrellus* is the most tolerant species. *E. serotinus* and *N. noctula* change in period A, from open land being the main factor at the location of recording, towards woods being important on a broader scale.

Summing up, the individual habitat requirements of the considered species vary with spatial scale. Though, trees are an important parameter on both scales.

Species habitat requirements on a temporal scale

To investigate variances in habitat use throughout the year recordings are divided into three periods. Species datasets are only sufficient in all periods for three species, *P. pipistrellus, P. nathusii* and *N. noctula*. Overall activity and species number is highest in period B. *P. pipistrellus* is tolerant towards all considered environmental variables in all periods and does not show a change of habitat requirements.

In *N. noctula* we see a transition, with open land on a small scale and woods in the 250m buffer being important in period A. In period B water represents an essential factor on a small scale, combined with urban variables on a larger scale. Woods are the main element shaping the Noctule’s habitat in period C.

P. nathusii shows a tendency towards urban elements in periods A and C, though not significantly. During period B green variables like open land, woods and trees are essential (Fig. 9 and 10).

E. serotinus depends in period A and B on rather natural structures like open land and trees, while *P. pygmaeus* tends slightly towards more urban elements (buildings, private land, noise). Both do not change their habitat requirements between periods A and B.

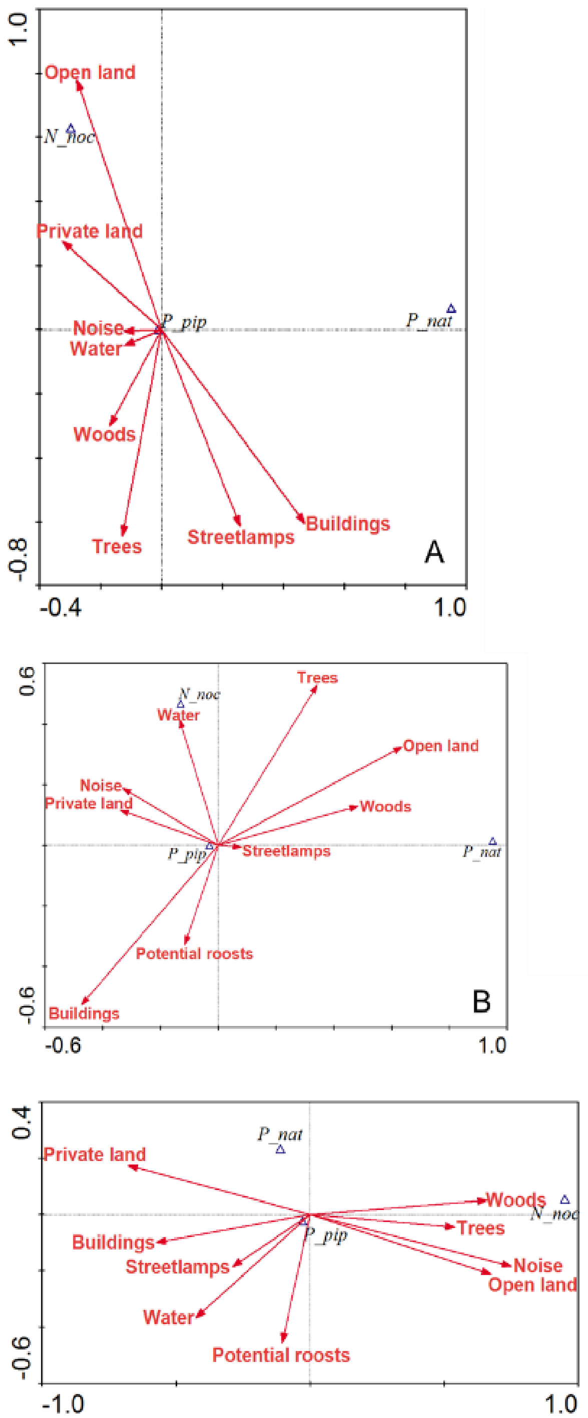

Figure 9 Habitat variables predicting activity of *P. pipistrellus, P. nathusii, N. noctula* over three periods in Buffer 100m

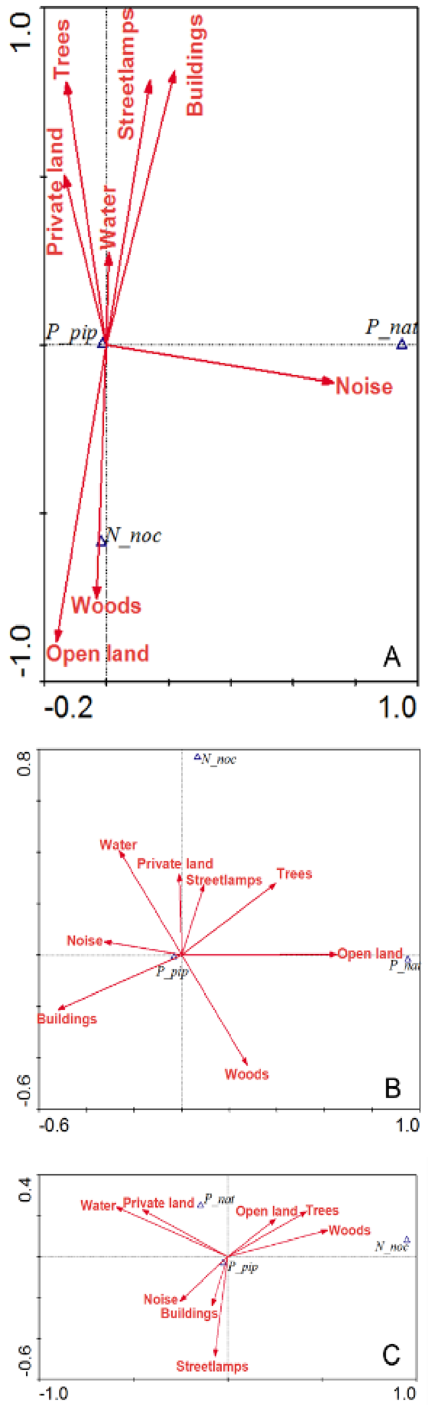

Figure 10 Habitat variables predicting activity of *P. pipistrellus, P. nathusii, N. noctula* over three periods in Buffer 250m

Discussion

Species richness

Overall the activity of ten species has been recorded in Utrecht. *P. pipistrellus* occurred at all study sites and showed the highest activity levels. This confirms it as a tolerant urban species, suggested by previous European studies (GAISLER ET AL. 1998, BARTONICKA & ZUKAL 2003, HALE ET AL. 2012, OBRIST ET AL. 2012, MASING 2013). *N. noctula, P. nathusii, P. pygmaeus* and *E. serotinus* are also frequently listed as similarly abundant urban species (ELZERMAN & BAERDEMAEKER 2010, MASING 2013). This study recorded *P. nathusii* at all but nine study sites, hence, indicating that it is widespread and relatively common species in Utrecht. Activity of *N. noctula* and *E. serotinus* was recorded at 49% and 38% of the study sites, respectively. However, this data do not necessarily indicate true differences in occurrence frequency between species due to varying detectability of species. Species like *P. pipistrellus, P. nathusii, E. serotinus* and *N. noctula* have rather loud and distinguishable echolocation calls. Therefore the chance of recording is higher compared to some *Myotis* species (JANSEN ET AL. 2012, ADAMS 2013).

Species numbers varied from one to eight per location. The study sites with an extraordinary number of species are partly located within very urbanised areas, hence our study does not provide evidence for a declining species richness from the city outskirts towards the central urban areas; this effect has been described by OPREA ET AL. (2009) and HALE ET AL. (2012). However, species requiring forests and being less tolerant to habitat disturbance and conversion, like *Myotis* species and *Plecotus auritus* (BOYD & STEBBINGS 1989), do occur only infrequently in urbanised habitats and then only in suburbs (GAISLER ET AL. 1998, GEHRT & CHELSVIG 2004, AVILA-FLORES & FENTON 2005). In the Netherlands 21 bat species have been recorded (www.vleermuis.net/bescherming/inleiding). Hence, half of the bat species known from the Netherlands occur within the urban area of Utrecht. However, of these ten species only six have been recorded in more than five locations and only four showed a high activity throughout the year. In fact, Utrecht offers habitats mainly to tolerant species adapted to strongly human-dominated landscapes. The presence of some rare species in the outskirts of Utrecht may be due to the availability of attractive foraging habitats such as open fields and pastures in the transition zone between the highly urbanised areas and the surrounding rural landscape. The absence of many species in urban areas may explain their decreasing abundances on a national level over the past decades, as the urbanisation impact increases (PEL-ROEST 2014).

For overall bat activity the availability of trees appears to be a key factor. For *P. pipistrellus,* the species with the highest activity in our study, HALE ET AL. (2012, 2015) found that networks of trees mitigate urbanisation effects even when gaps within this network occur. Further JONKER ET AL. (2010) state the common pipistrelle is drawn to urban areas with a sufficient tree cover. Since trees do not only provide roost sites for some species and foraging sites for most, but can additionally mark linear commuting routes, their importance in urban areas has repeatedly been emphasised for urban species (VERBOOM & HUITEMA 1997, JANSEN ET AL. 2012, HALE ET AL. 2012 & 2015, KUSCH & SCHMITZ 2013).

Species habitat requirements

As indicated by our study some environmental variables like sealed ground, noise, number of streetlamps and water do hardly have any detectable effects on the activity of bats present in the urban environment. First of all, this may be due to the generally high spatial cover of these habitat types and the high density of streetlamps throughout the city. Second, this study was conducted on a microhabitat scale, not including study sites beyond the urban area for comparison. Yet, these factors may still influence the absence of other species.

BIHARI & BAKOS (2001) state that even a high and permanent noise level does not affect the choice of roost sites in Noctule bats. We cannot identify a significant negative correlation of noise and bat presence for any of the considered species. Interestingly also the number of streetlamps did not show any effect. Though many studies (e.g. RYDELL 1992, PATRIARCA & DEBERNARDI 2010, LEWANZIK & VOIGT 2013) have been carried out to investigate the effect of light on nocturnal fauna, our results do not prove a negative effect of a high number of streetlamps on certain species, nor do they show a positive effect on species known to forage at light sources. GAISLER ET AL. (1998) also discovered no correlation between streetlamps and bat presence. Streetlamps are not the sole indicator for light pollution, but species abundant in urban areas apparently have adapted to the presence of light sources. Though, this refers to general bat activity while roosts are preferred in dark surrounding (PATRIARCA & DEBENARDI 2010). One of the surrogate variables for urbanisation is the area covered by buildings. We expected a relationship between availability of buildings and the activity of species, such as *E. serotinus, P. pipistrellus* or *V. murinus*, roosting in these artificial structures. However, we were only able to prove this for the latter.

That waterbodies do not play a major role in explaining differences in bat activity between study sites is probably related to their high availability in most parts of Utrecht, thereby decreasing the importance of single water sources (GEHRT & CHELSVIG 2003). Yet, the occurrence/activity of *M. daubentonii*, a species known to forage over water, is positively related to the presence of waterbodies (GAISLER ET AL. 1998, BARTONICKA & ZUKAL 2003). Interestingly *N. noctula*, a rather large tree roosting species, chooses habitats with a high water cover during lactation. This could infer that insect abundances near water are exploited when energy demands during nursery are high.

Surprisingly and contrary to previous studies (e.g. LEGAKIS ET AL. 2000, DAVIES ET AL. 2012) small scale and heterogeneous green structures like gardens did not significantly affect the activity of bat species in our study. This might be due to the high availability of these habitats in all study areas, since recordings took place in gardens of housing areas.

In contrast green structures like wooded areas and an increasing number of trees had a positive impact on species richness and activity. In general the number of trees proved to better explain varying bat activity than wooded area. This may indicate that a high number of trees distributed across the study area is superior to larger continuous patches of woods for species capable of colonising urbanised areas. Though wooded areas prove to be important to *N. noctula*, mainly during pregnancy and mating, and *P. nathusii*, both predominantly roosting in trees (BERG & WACHLIN 2004B, DIETZ ET AL. 2007, LUNDY ET AL. 2010, JANSEN ET AL. 2012).

The correlation of the Nathusius' activity with the presence of open land is rather surprising since the species is known to roost in woods and forage in riparian or wooded habitats (BERG & WACHLIN 2004B, DIETZ ET AL. 2007, FLAQUER ET AL. 2009, GEYSELING ET AL. 2009, LUNDY ET AL. 2010, GELHAUS & ZAHN 2010, JANSEN ET AL. 2012, HARGREAVES ET AL. 2015). However, as foraging routes frequently follow forest edges or treelines the vicinity to open land may be often a logical consequence, although this habitat type itself may not play a significant role for foraging. We certainly expected a correlation of open areas with the occurrence of *E. serotinus*, one of the few native bat species less reliant on treelines and shrubs on flight routes and even hunting large beetles over fields, pastures, meadows and lawns (CATTO ET AL. 1996, ROBINSON & STEBBINGS 1997, VAUGHAN ET AL. 1997, VERBOOM & HUITEMA 1997, BERG & WACHLIN 2004A, CIECHANOWSKI ET AL. 2007, KERVYN & LIBOIS 2008, TEIGE 2009, ZUKAL & GAJDOSIK 2012, ARTHUR ET AL. 2014, TINK 2014). Contrary, our study does not highlight *E. serotinus* frequenting open areas. *N. noctula*, similar in size, is able to master large distances, also across open areas. Therefore it is not surprising that the proportion of open areas plays at least a minor role. Another species foraging over open land is *V. murinus*, and for this species we can accordingly demonstrate a correlation of its activity with open areas (DIETZ ET AL. 2007).

For all variables only their quantity and structure and never their quality was examined. Therefore detailed further research will be necessary to improve our understanding on the importance of individual habitat variables for bats in urban landscapes.

Spatial scale

Our study only considered habitat types and structures within a 100m and 250m buffer around installed bat recorders. However, the range used by bats is much larger than this; distances between roosts and foraging sites can even exceed several kilometres, especially in larger species like *N. noctula* and *E. serotinus*. .

For *P. pygmaeus, P. auritus, M. dasycneme* and *Myotis mystacinus* datasets are rather limited or no significant preferences towards certain habitat types or structures were revealed. *P. pipistrellus* proved to be very tolerant towards the environmental variables on all scales considered in this study. *E. serotinus* showed a tendency from urban parameters on a smaller scale towards trees and open land on a larger scale. This may indicate activity recordings near roosting sites in urban environment with foraging habitat in a landscape shaped by green structures in the vicinity. *V. murinus, P. nathusii* and *N. noctula* revealed no differences in habitat requirements between the two studied spatial scales; wooded areas/trees and open land are needed on a smaller and larger scale. In *M. daubentonii* a preference for waterbodies is indicated for both spatial scales, while on a larger scale the availability of wooded areas gained in importance. This classifies *M. daubentonii* as a species inhabiting rather natural habitats, foraging near water and roosting in trees (DIETZ ET AL. 2007).

Temporal scale

Since bats are not only mobile but also follow an annual reproductive cycle accompanied by a change of roosting sites, habitat requirements have to be evaluated also on a temporal scale. Considering not only activity but also recorded species numbers, overall bat activity was highest in period B, the phase of nursery and introducing juveniles to a variety of roosts (DIETZ ET AL. 2007). Maternity is in many species accompanied by a higher number of foraging flights but shorter flight distances and subsequently followed by migration and roost switching (BAGGOE 2001, RUSS ET AL. 2001, RUSS & MONTGOMERY 2002, DAVIDSON-WATTS ET AL. 2006, GELHAUS ET AL. 2010, LOPEZ-ROIG & SERRA-COBO 2014). Throughout the year *P. pipistrellus* proved to be the most tolerant species, not showing seasonal changes in habitat requirements. In contrast, data for *P. nathusii* indicate differences in habitat requirements between survey periods. During spring urban structures played a key role while in summer open land and wooded area/trees were preferred. This change of habitat use in the Nathusius' pipistrelle is remarkable since it is a long distance migrating species. Maternity roosts are not in the Netherlands but rather in north-eastern Europe. Therefore mainly male individuals are present during summer. Females migrate to the Netherlands for mating and hibernation in autumn and leave again in spring (BARLOW & JONES 1996, BERG & WACHLIN 2004B, PEL-ROEST 2014, HARGREAVES ET AL. 2015). For *N. noctula* rather green structures are essential throughout the year. Contrary to period A and C woods were less important during lactation period when water and urban structures gained in importance. As we did find different habitat requirements on a temporal scale and changes in activity, we have to contradict BARTONICKA'S & ZUKAL'S (2003) findings of no seasonal differences "in the level of activity and habitat use".

Conservation implications

Our study shows, that urban areas are inhabited by several bat species, yet only species proven to be tolerant towards urban variables occur frequently. Species of high conservation interest (as thought to be rather specialised and rare) tend to avoid urbanised landscapes. However, since all abundant bat species are legally protected and population trends are widely unknown, a focus in urban planning should be drawn towards the accessibility of urban areas.

First of all, we proved trees to be a very important habitat structure for all occurring species. Whether they are used as roosting sites, foraging habitats or as guidance along flightpaths we can only guess, and their function may be species specific. Yet, the fact that an increasing number of trees in an urban area influences the species richness positively should not be ignored in urban planning. Further we advise to take the importance of a variety of green structures spread across the city into account. Bats as mobile animals reach different habitat patches rather easily, and require to do so.

Additionally, bats' seasonality has to be considered when urban planning might negatively impact habitats. As we found variation in habitat requirements, the temporal shifting of projects into different seasons may mitigate the effect on bat populations. Here, further species specific research on seasonal variation in habitat use needs to be conducted.

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Appendix

Appendix Table 1 Results of Mann-Whitney U-test testing for differences of locations with and without recorded activity of *V. murinus*, *P. pygmaeus*, *P. auritus* and *M. daubentonii* (n.s. = not significant)

	Sealed area	Buildings	Street-lamps	Noise min	Noise max	Private land	Wooded area	Trees	Open land	Water-bodies
50m										
Vmur	n.s.	0.00215	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Ppyg	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Paur	n.s.	n.s.	n.s.	0.03718	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Mdau	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.01854
100m										
Vmur	n.s.	0.00391	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Ppyg	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Paur	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Mdau	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.02805	0.00847
250m										
Vmur	n.s.	0.01942	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.04524	n.s.
Ppyg	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Paur	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Mdau	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
500m										
Vmur	n.s.	0.02888	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.01453	n.s.
Ppyg	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Paur	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Mdau	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.00707	n.s.	n.s.

Appendix Table 2 Results of Spearman-Rank-Correlation relating species activity (*E. serotinus, N. noctula, P. nathusii and P. pipistrellus*) to environmental variables (n.s. = not significant)

	Sealed area	Buildings	Street-lamps	Noise min	Noise max	Private land	Wooded area	Trees	Open land	Water-bodies
50m										
Eser	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Nnoc	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.23043	n.s.
Pnat	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.24141	n.s.	n.s.	n.s.
Ppip	n.s.	-0.29009	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.22546	n.s.
100m										
Eser	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.31208	0.24082	n.s.	n.s.
Nnoc	n.s.	-0.23620	n.s.	n.s.	n.s.	-0.24648	0.24041	n.s.	0.28253	n.s.
Pnat	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Ppip	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
250m										
Eser	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.30477	n.s.	n.s.
Nnoc	n.s.	n.s.	n.s.	n.s.	n.s.	-0.25862	n.s.	0.23961	0.23432	n.s.
Pnat	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Ppip	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

500m										
Eser	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Nnoc	n.s.	n.s.	0.23884	n.s.	n.s.	n.s.	n.s.	0.26620	n.s.	n.s.
Pnat	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Ppip	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Appendix Table 3 Results of pairwise Spearman-Rank-Correlation of landscape variables quantified for 100 m and 250 m buffers around survey points, correlation coefficients >0.50 (n.s. = not significant)

	Water-bodies	Buildings	Open area	Wooded area	Private land	Trees	Noise min	Street-lamps	Roost trees	Sealed ground
Waterbodies		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-0.536
Buildings	n.s.		-0.795	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Open area	n.s.	-0.680		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Wooded area	n.s.	n.s.	n.s.		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Private land	n.s.	n.s.		n.s.		n.s.	n.s.	n.s.	n.s.	-0.560
Trees	n.s.	n.s.	0.561	n.s.	n.s.		n.s.	n.s.	n.s.	n.s.
Noise min	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.		n.s.	n.s.	n.s.
Streetlamps	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.		n.s.	n.s.
Roost trees	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.		n.s.
Sealed ground	n.s.	n.s.	n.s.	n.s.	-0.632	n.s.	n.s.	n.s.	n.s.	

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