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Modern technology owes ecology an apology

~ Alan M. Eddison ~

Abstract

Urbanisation is one of the biggest environmental challenges of our modern world for biodiversity conservation. Beside loss and degradation of natural habitats, it causes high levels of disturbance due to human activities and increases the exposure of organisms to pollutants such as noise, night-time lights or chemicals. Hence, the urban landscape seems to offer few favourable habitats for avian wildlife.

Indeed, studies along urban-rural gradients show declining bird species numbers and changes in species composition from urban outskirts to city centres. However, quantifying the degree of urbanisation within city borders is intricate as urban ecosystems are characterised by complex interactions between social, economic and environmental variables. We evaluated the potential of night-time satellite images as a tool to integrate the large set of urbanisation metrics such as land use data or demographic measures into a single variable for assessing anthropogenic impact and its associated consequences on avian diversity.

Light pollution has also been found to have profound effects on the timing of daily activity patterns in birds. In one of our studies we analysed to what extent artificial illumination differentially affects bird species with different visual capabilities, using their eye size as proxy. Until now to our knowledge no study included these two variables, light pollution and eye size, in multivariate analysis to test for their additive effects on birds' daily activity patterns. Light pollution was quantified at two spatial scales. Besides measuring sky brightness and light intensity at the survey point level, night-time satellite images were used to quantify light pollution on a regional scale. In contrast to most of the other studies testing for effects of light pollution on activity patterns of birds, our study did not only focus on the singing behaviour. Rather, the start of bird activity was recorded during winter.

Within the hostile urban matrix city parks represent hotspots of avian diversity. Therefore, identifying the key drivers for avian diversity within these urban green spaces is essential to ensure effective management measures. Thus, a further three studies analysed which city park characteristics promote functional diversity of bird communities and the occurrence of forest bird species such as woodpeckers and raptors. Whereas most studies on urban birds in city parks rely on surveys during breeding time, mainly covering one season, we used long-term data on wintering birds.

To test for effects of light pollution and eye size on the activity start of birds, point counts were carried out between November 2014 and April 2015 at 84 randomly selected survey points within the city borders of Vienna. All other studies rely on bird surveys being carried out in up to 36 city parks of Vienna, covering up to seven winters.

The results of our studies on the urban ecology of birds in Vienna show that altered light regimes in cities cause changes in the morning activity of birds. Moreover, the timing of activity patterns proved to be related to interspecific variations in eye size. Hence, light pollution could contribute to shape bird communities inhabiting urban environments if large-eyed birds benefit disproportionately from an earlier activity start in light polluted habitats.

As for the breeding season, results reveal park size as the key driver for avian diversity within city parks during winter. Thereby, park area positively affects not only taxonomic but also functional diversity of bird communities. Furthermore, also specialist forest bird species such as Great Spotted Woodpecker, Middle Spotted Woodpecker and Eurasian Sparrowhawk benefit from large parks during the non-breeding season. Additionally, city parks embedded in a highly urbanised matrix show lower taxonomic

and functional avian diversity. Hence, to preserve avian diversity within urban landscapes large city parks are of prime importance. As in cities an enlargement of city parks is difficult to realise, the implementation and maintenance of corridors such as alley trees along roads or scattered greenery may be a feasible alternative. Besides representing hot spots of biodiversity city parks embedded in a highly permeable urban matrix could also help to facilitate functional diverse bird assemblages and may represent important refuges for specialist forest birds during winter. As a consequence, they may contribute to promote and maintain biodiversity and ecosystem functions in our modern human-dominated landscapes.

Zusammenfassung

Urbanisierung stellt in unserer modernen Welt eine der größten Herausforderungen für den Schutz der Biodiversität dar. Neben dem Verlust und der Entwertung natürlicher Habitate, bringt sie ein hohes Maß an menschlicher Störung mit sich und setzt Organismen vermehrt Schadstoffen wie Lärm, nächtlicher Beleuchtung oder Chemikalien aus. Das städtische Umfeld scheint daher wenig attraktiv für die Vogelwelt zu sein.

Tatsächlich zeigen Studien entlang von Urbanisierungsgradienten mit zunehmender Verstädterung eine Abnahme des Artenreichtums und eine Änderung in der Artenzusammensetzung von Vogelgemeinschaften. Den Urbanisierungsgrad im Rahmen solcher Studien zu quantifizieren ist schwierig, da städtische Ökosysteme durch komplexe Wechselbeziehungen sozialer, ökonomischer und ökologischer Einflussfaktoren charakterisiert sind. Wir untersuchten, ob Nachtlicht-Satellitenaufnahmen als integratives Maß für Urbanisierung genutzt werden können, um den menschlichen Einfluss und die damit verbundenen Konsequenzen auf den Artenreichtum von Vögeln zu erfassen.

Lichtverschmutzung kann bei Vögeln eine zeitliche Verschiebung der täglichen Aktivitätsmuster verursachen. In einer weiteren Studie untersuchten wir, inwieweit dieser Effekt der Lichtverschmutzung von der Augengröße einzelner Vogelarten – als Indikator für visuelle Leistungsfähigkeit unter geringen Lichtintensitäten – abhängig ist. Unseres Wissens hat bisher noch keine Studie Lichtverschmutzung und Augengröße in multivariate Analysen integriert, um additive Effekte dieser beiden Variablen zu testen. Lichtverschmutzung wurde auf Basis zweier räumlicher Skalen erhoben: Neben Messungen von Himmelshelligkeit und Lichtintensität an den Kartierungspunkten, wurde Lichtverschmutzung auf regionaler Ebene anhand von Nachtlicht-Satellitenaufnahmen quantifiziert. Im Gegensatz zu den meisten anderen Studien, die die Effekte von Lichtverschmutzung auf den Aktivitätsbeginn von Vögeln untersuchten, berücksichtigte unsere Studie nicht nur die Gesangsaktivität, sondern fokussierte vielmehr auf den Aktivitätsbeginn während der Wintermonate.

Innerhalb der, für die Avifauna unbehaglichen urbanen Matrix stellen Stadtparks Kerngebiete des Artenreichtums dar. Umso wichtiger ist es, Parameter, die den Artenreichtum dieser städtischen Grünflächen positiv beeinflussen, zu identifizieren. Nur dann können effiziente Managementmaßnahmen eingeleitet werden. Entsprechend untersuchten drei weitere Studien, welche Stadtparkcharakteristika die funktionelle Diversität von Vogelgemeinschaften sowie das Vorkommen von Waldarten wie Spechten und Greifvögeln fördern. Während die meisten Studien zur Avifauna in Stadtparks auf Kartierungen während der Brutzeit beruhen und überwiegend nur eine Saison abdecken, verwendeten wir Langzeitdaten überwinternder Vögel.

Um den Effekt von Lichtverschmutzung und Augengröße auf den Aktivitätsbeginn von Vögeln zu untersuchen, wurden auf Wiener Stadtgebiet zwischen November 2014 und April 2015 an 84 zufällig ausge-

wählten Kartierungspunkten Punkttaxierungen durchgeführt. Alle anderen Studien basieren auf Vogel-erhebungen, die bis zu 36 Stadtparks und bis zu sieben Winter abdecken.

Die Ergebnisse unserer Studien zur Stadtökologie von Vögeln in Wien zeigen, dass nächtliche Beleuchtung den morgendlichen Aktivitätsbeginn von Vögeln beeinflusst. Gleichzeitig ist der Aktivitätsbeginn auch von zwischenartlichen Unterschieden in der Augengröße abhängig. Daher könnte Lichtverschmutzung die Zusammensetzung von urbanen Vogelgemeinschaften beeinflussen, falls Vögel mit großen Augen überproportional von einem früheren Aktivitätsbeginn in lichtverschmutzten Habitaten profitieren.

Wie Studien bereits für die Brutsaison zeigten, stellt auch während der Wintermonate Parkgröße die treibende Kraft für den Vogelreichtum in Stadtparks dar. Mit zunehmender Parkgröße wird dabei nicht nur der Artenreichtum, sondern auch die funktionelle Diversität von Vogelgemeinschaften positiv beeinflusst. Des Weiteren profitieren im Winter auch spezialisierte Waldvogelarten wie Buntspecht, Mittelspecht und Sperber von großen Parks. Stadtparks, die hingegen in eine stark urbanisierte Matrix eingebettet sind, weisen geringe taxonomische und funktionelle Diversität in ihren Vogelgemeinschaften auf. Um daher den Vogelreichtum in der urbanen Landschaft zu bewahren sind große Stadtparks von wesentlicher Bedeutung. Da in Städten eine Vergrößerung von Stadtparks schwer zu realisieren ist, könnte die Einführung und Erhaltung von Korridoren wie Baumalleen entlang von Straßen oder eingestreute Grünflächen eine mögliche Alternative darstellen. Stadtparks, die in eine derart durchlässige Matrix eingebettet sind, fungieren dann nicht nur als Hotspots der Biodiversität, sondern fördern auch funktionell diverse Vogelgemeinschaften und bieten spezialisierten Waldvogelarten im Winter wichtige Zufluchtsorte. Sie tragen damit zur Förderung und Erhaltung von Biodiversität und Ökosystemfunktionen in unserer modernen, vom Menschen dominierten Landschaft bei.



1. General Introduction

More than 55 % of the world's population lives in urban areas and demographic projections predict that this proportion will continue to grow rapidly, reaching 68 % by 2050 (UN DESA 2018). Thereby, citizens are increasingly moving away from city centres. Rather, they tend to redistribute themselves in a suburban or exurban pattern, causing cities to grow in area much faster than in population (Marzluff et al. 2001). This urban sprawl turns native environment into a patchwork of similar land-cover types throughout the world including residential, commercial, industrial and recreational sites, being connected by roads and railways (Niemelä 2011). Beside loss and degradation of natural habitats, this land use conversion causes higher levels of disturbance due to human activity (Fernández-Juricic et al. 2001), induces changes in climatic conditions (Hart & Sailor 2009) and increases the exposure to pollutants such as noise, light or chemicals (Rodríguez Martín et al. 2015). Consequently, urban areas seem to offer few favourable conditions for flora and fauna (Croci et al. 2008). Indeed, studies testing for effects of urbanisation on biodiversity patterns indicate decreasing species numbers with increasing urbanisation across several groups of organisms such as plants, insects, amphibians and mammals (Parris 2006, Clark et al. 2007, Cavia et al. 2009, Melliger et al. 2018). Also in birds, studies along urban-rural gradients show declining species numbers and changes in species composition from outskirts to city centres (Clergeau et al. 2006, Ortega-Álvarez & MacGregor-Fors 2009, Suarez-Rubio et al. 2016). Thereby, urban exploiters (or synanthropic species) are adapted to the intensely modified habitats at the urban core and strongly depend on human resources. The combination of reduced predators, altered climatic conditions and abundant food subsidies allow them to develop dense and stable populations (Marzluff 2001, McKinney 2002, 2006). Because of the uniform nature of cities worldwide – being constructed to satisfy the relatively narrow demands of human beings – assemblages of urban exploiters consist of a very small subset of the world's species and represent one of the most homogenized biotas (Blair 2001, McKinney 2002, 2006). Suburban or urban fringe habitats are occupied by urban adapters, which largely consist of forest species from nearby ecosystems, utilising green space remnants available in the urban landscape such as gardens or forest fragments (McKinney 2002, 2006). Thereby, city parks are among the most species rich types of urban green spaces and serve as strongholds for avian diversity within the otherwise hostile urban matrix (Ikin et al. 2013, Strohbach et al. 2013, Forman 2014, Nielsen et al. 2014). Hence, to ensure or even enhance bird diversity within the urban landscape an effective management of urban parks is required. Therefore, in a first step identifying the key drivers for promoting avian diversity within city parks is essential. Three manuscripts of my PhD-thesis analyse which city park characteristics positively affect taxonomical as well as functional diversity of bird communities and which parameters enhance the occurrence probability of forest bird species such as woodpeckers and raptors. Whereas most studies on urban birds in city parks of the temperate region rely on surveys during breeding time, mainly covering one season, we used long-term data on wintering birds (see chapter 2.1.-2.3.).

Studies trying to identify key drivers of bird diversity within city parks do not only focus on local habitat characteristics of such green spaces. Rather, they also try to quantify the urbanisation degree of the matrix surrounding city parks. However, this turns out to be challenging as urban ecosystems are characterized by complex interactions between social, economic and environmental variables (Alberti 2005). To cover these different facets of urban development a high diversity of potentially important variables can be considered such as land use data, landscape metrics, demographic measures or traffic intensity (McIntyre et al. 2000). Selecting an appropriate subset among all these variables that best captures the variability in the urban landscape is challenging and limited by the high correlation between these interacting variables (Hahs & McDonnell 2006). However, light pollution measures have already been found to be connected to demographic and economic values (Ma et al. 2014, Shi et al. 2014) and also serve as useful tools in the conservation management of single species and whole

ecosystems (Aubrecht et al. 2010, Mazor et al. 2013). Hence, in another study we evaluated the potential of night-time satellite images as a tool to integrate the large set of urbanisation metrics such as land use data or demographic measures into a single variable for assessing anthropogenic impact and its associated consequences on avian biodiversity (see chapter 2.4.).

Night-time light pollution is expanding worldwide due to ongoing urbanisation and increasing standard of living (Gil & Brumm 2014). As most birds possess excellent light perception, artificial night lighting affects them in various ways. Besides having attracting effects on night migrating birds, increasing nocturnal activity or causing changes in the seasonal timing, light pollution also alters the timing of daily activity (Posch et al. 2013, Gil & Brum 2014). The onset of daily activity is also related to interspecific variation in eye size (Ockendon et al. 2009). However, until now to our knowledge no study included these two variables, light pollution and eye size, in multivariate analysis to test for their additive effects on birds' daily activity patterns. In contrast to most of the other studies testing for effects of light pollution on activity patterns of birds, our study did not only focus on the singing behaviour. Rather, the start of bird activity was recorded during winter (see chapter 2.5., for a new method of measuring the avian eye size see chapter 2.6.).

Results of our studies may expand the existing knowledge about the effects of light pollution on birds by focussing on the non-breeding season. Furthermore, local and regional determinants promoting the capability of city parks as refuges for birds during cold winters will be identified. This is of particular importance as the quality of wintering habitats can be linked with the physical condition of birds at the end of winter (Bearhop et al. 2004, Tellería & Pérez-Tris 2004). Consequently, suitable habitat conditions during winter may not only facilitate survival under harsh weather conditions, but may even increase the reproductive success of birds in the subsequent breeding season as birds in good body condition prior to incubation show larger clutch sizes, advanced laying dates and higher fledgling success (Reynolds et al. 2003, Robb et al. 2008). Hence, results may help to maintain avian diversity within the urban landscape – a landscape already heavily suffering from biodiversity losses and showing continuously growing demands for more built-up areas.

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2. Publications and submitted manuscripts

2.1. Functional diversity of urban bird communities: effects of landscape composition, green space area and vegetation cover

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Abstract

In this study, we aim to gain a better insight on how habitat filtering due to urbanization shapes bird communities of Vienna city parks. This may help to derive implications for urban planning in order to promote and maintain high diversity and ecosystem function in an increasing urbanized environment. The structure of wintering bird communities of 36 Vienna city parks – surveyed once a month in January 2009, December 2009, December 2012, and January 2013 – was described by species richness and the functional diversity measurements FRic (functional richness), FEve (functional evenness), and FDiv (functional divergence). Environmental filtering was quantified by park size, canopy heterogeneity within the park, and the proportion of sealed area surrounding each park. Species richness, FRic, and FDiv increased with increasing park size. Sealed area had a strong negative effect on species richness and FDiv. Canopy heterogeneity played a minor role in explaining variance in FDiv data. FEve did not respond to any of these park parameters. Our results suggest a loss of species richness and functional diversity, hence most likely indicate a decline in ecosystem function, with decreasing park size and increasing sealed area of the surrounding urban landscape matrix.

Keywords

Avifaunal richness, ecological function, environmental filter, landscape composition, tree cover, urban birds, urban ecology, urban green area

Own contribution

Study design: 50 %, data collection: 50 %, statistical analyses: 100 %, manuscript preparation: 100 %

Introduction

As the human population is continuously growing, landscapes are increasingly affected by urbanization. In 2010, more than 50 % of the world population inhabited urban areas, and by 2050, even 70 % of the human population are expected to live in cities (UN 2012). This ongoing urban development leads to a fragmentation, isolation, and degradation of natural habitats, being accompanied by severe impacts on the biotic communities living in urban environments (Alberti 2005; McKinney 2006), such as arthropods (Bergerot et al. 2011; Vergnes et al. 2012), reptiles and amphibians (Hamer and McDonnell 2010), or small mammals (Gomes et al. 2011).

Numerous studies on urban bird communities have also already shown that urbanization can cause changes in community composition, a decrease in species richness, and a loss of species diversity (Marzluff 2001; Chace and Walsh 2006; Reis et al. 2012; Yu and Guo 2013; Ferenc et al. 2014). Urbanization acts as an environmental filter, resulting in higher functional similarity of bird community with increasing urbanization (Croci et al. 2008; Meffert and Dziock 2013; Sol et al. 2014). Although all these studies report a decrease in functional diversity due to urbanization, these results are heterogeneous, often lacking standard and well-known indices (Filippi-Codaccioni et al. 2009). Additionally, Mason et al. (2005) argued that functional diversity cannot be quantified by a single index. To consider the different facets of functional diversity, the indices FRic (functional richness), FEve (functional evenness), and FDiv (functional divergence) were proposed, as they are continuous, abundance based (FEve, FDiv), incorporate multiple functional traits, and are independent of species richness (FEve, FDiv) and of each other (Villéger et al. 2008; Mouchet et al. 2010). FRic is used for quantifying the niche space filled by a community (Villéger et al. 2008). Functional evenness describes the evenness of abundance distribution of species in a niche space (Villéger et al. 2008). FDiv represents the abundance distribution within the functional trait space occupied by a community (Villéger et al. 2008). The first studies testing how these different facets of functional diversity respond to habitat and landscape modification have already shown that habitat filtering can shape bird communities in fragmented systems (Filippi-Codaccioni et al. 2009; Ding et al. 2013; Barbaro et al. 2014).

Birds are particularly suitable to analyze functional diversity patterns as there is comprehensive information available on their biological characteristics (e.g., Glutz von Blotzheim 1985–1999; Dunning 2008), which is essential when working with functional diversity measurements based on morphological, physiological, and behavioral traits.

In our study, environmental filtering will be characterized at two spatial scales. On a local scale, the city park characteristics park size and canopy heterogeneity will be considered. Park size has already been identified to be one of the most important factors influencing bird diversity and community composition in city parks with larger parks showing higher taxonomic and functional avian diversity than smaller ones due to an increase in habitat complexity (Jokimäki 1999; Fernández-Juricic 2000a; Fernández-Juricic and Jokimäki 2001). As in geographical regions naturally covered by forest, city parks with high amounts of woody vegetation are predominantly inhabited by forest birds and vegetation variables such as foliage cover, tree height, or area of woodlot often play an important role (Jokimäki 1999; MacGregor-Fors 2008). In our study, canopy heterogeneity (perimeter of closed canopy/area of closed canopy) of city parks – as size independent vegetation variable – will be considered. A high degree of canopy heterogeneity indicates a higher fragmentation of tree cover within a city park and may influence functional diversity of bird communities, as species being habituated to human activities are known to be edge specialists, whereas species with specific habitat requirements depend on the interior areas of closed woodlot (Fernández-Juricic 2001). On a landscape scale, we expect that environmental filtering will be driven by the urban matrix adjacent to each city park, which can modify

connectivity of remaining green spaces. Landscape connectivity, defined as the “degree to which the landscapes facilitate or impede movement among resource patches” (Tischendorf and Fahrig 2000), can be a key factor for maintaining species diversity in fragmented landscapes (Martensen et al. 2008; Shanahan et al. 2011). As a result, also city parks surrounded by a less urbanized landscape show higher numbers of bird species and individuals, attracting especially woodland species, insectivores, and cavity nesting birds (Carbó-Ramírez and Zuria 2011; Ikin et al. 2013).

This study examines how habitat filtering due to urbanization influences functional trait distributions and as a consequence structures bird communities of Vienna city parks. Therefore, species richness and the three functional diversity indices FRic, FEve, and FDiv will be used to gain a better insight on the influence of environmental filters shaping bird communities of human-dominated landscapes (Villegger et al. 2008). In accordance with the results of other studies (Reis et al. 2012; Yu and Guo 2013), we also expect a loss of species diversity with increasing urbanization. Furthermore, we predict a decrease in FRic with increasing urbanization, due to increased functional similarity of bird species in highly urbanized areas (Luck and Smallbone 2011; Meffert and Dziok 2013). Birds vary in their ability to adapt to changes along the urban–rural gradient, with urbanization filtering for species based on their biological traits (McKinney 2002; Chace and Walsh 2006). Hence, with increasing urbanization, we expect a functionally more concentrated distribution of species within functional space, leading to a decrease in FDiv. A few dominant species possess superior abilities for living in urban environments, become even dependent on urban resources, and peak in their abundances in the urban core area (McKinney 2002). Therefore, we expect a decrease in FEve with a higher degree of urbanization.

Materials and Methods

Study area

The study was carried out in Vienna (48°13' N, 16°22' E), the capital city of Austria, located at the northeastern extension of the Alps and predominantly situated within the Vienna Basin (Berger and Ehrendorfer 2011). A total of 208.42 km² (50.2 %) of the city area is not built-up. Nearly 6 % consist of city parks and other man-made green space. Bird communities were assessed in 36 city parks, ranging from 0.4 ha to 34.5 ha in size and spread across the built-up area of Vienna, southwest of the river Danube (Fig. 1).

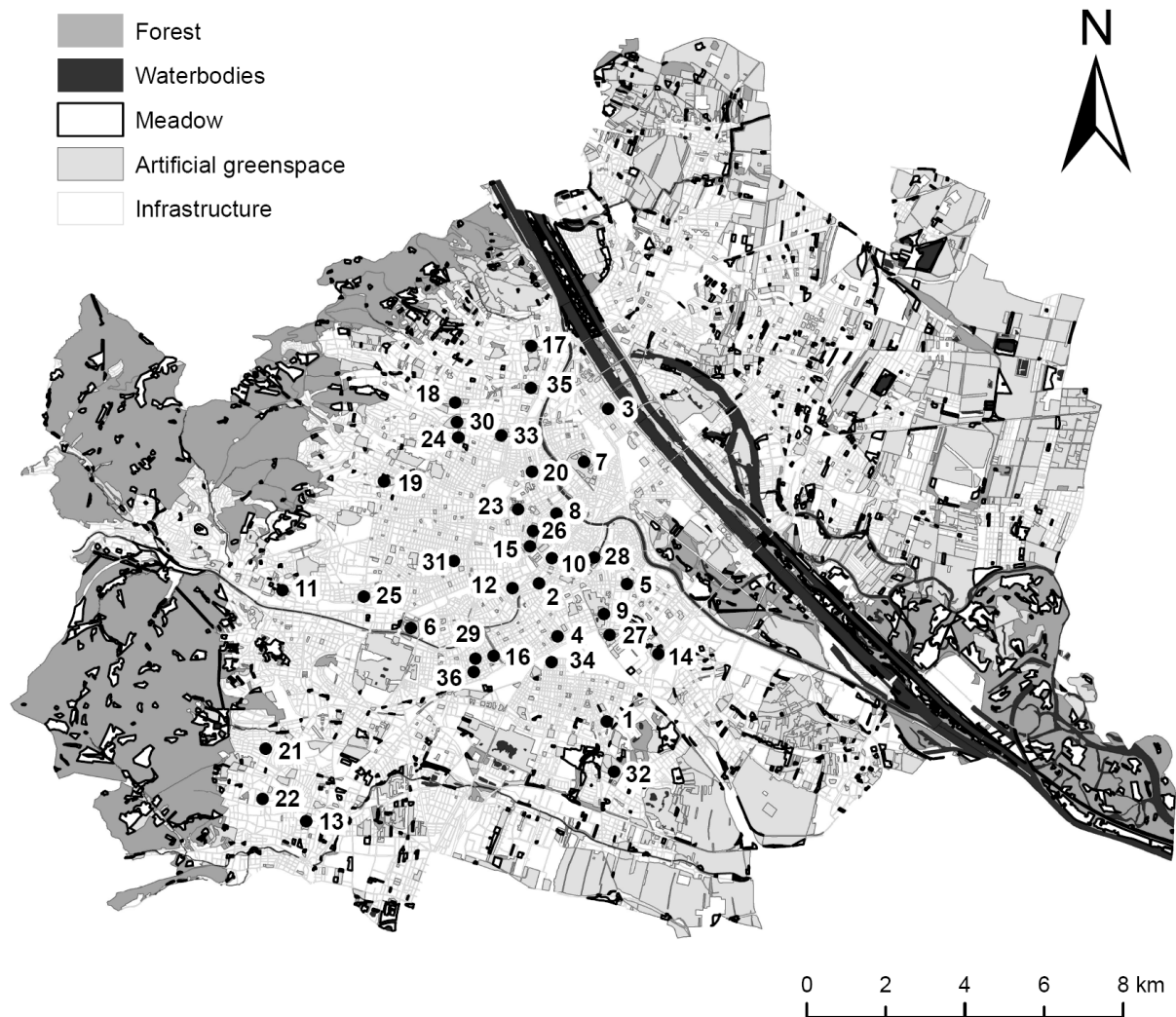


Figure 1. Overview on 36 city parks of Vienna where bird surveys were carried out. Black circles indicate the midpoint of each city park; city park codes refer to Table S1.

Quantification of city park habitat variables and urban matrix

For each city park, area and tree cover were considered. Park size was calculated in ArcGIS 10.0 (ESRI, Redlands, CA, USA) based on Vienna land use data of the year 2009 (Table S1). Tree cover of each city park was digitized in ArcGIS 10.0 (ESRI) using satellite images of the map service “ArcGIS Online basemaps” (0.3-m spatial resolution, date of origin: August 2011). For calculating the canopy cover heterogeneity of each city park, the perimeter of digitized canopy (m) was divided by the area of closed canopy (m²), defined as closed leaf cover tolerating gaps up to 5 m (Table S1). The urban landscape surrounding each city park was described based on Vienna land use data from the period 2010 to 2012. In ArcGIS 10.0 (ESRI), a circle with a radius of 500 m – centered on the centroid of each park – was clipped out of the land use shape file. Then, the 55 categories of the land use data were simplified to four categories, describing the permeability of the landscape for avifauna: natural green space (e.g., pasture), manmade green space (e.g., lawn, meadow, and other unsealed areas), sealed areas (e.g., roads, buildings), and forest/tree-covered areas. For each land use category, the area within the circle was calculated, excluding the park area. The proportion of the park area within the circle of radius 500 m varied between 0.5 % for the smallest park (Börsepark: 0.4 ha) and 44 % for the largest park (Augarten: 34.5 ha).

Bird surveys

Available data on wintering bird communities of Vienna city parks – covering 3 years – were used. Bird surveys were carried out by groups averagely consisting of at least one experienced field ornithologist, being assisted by three further observers. Surveys were conducted once a month in January 2009, December 2009, December 2012, and January 2013. Each park was surveyed between 08:00 AM and 15:30 PM under good weather conditions (i.e., avoiding windy days and/or days of heavy rain and snowfall, respectively). Sampling effort was standardized according to park size (10 min per 1 ha). The existing road network within a park was used for survey routes, trying to cover the entire area of the park in a zigzag manner. Carrying out surveys from existing roads may cause samples unrepresentative of the surrounding area because of greater disturbance and presence of “edge habitats” close to the roads (Buckland et al. 2008). However, the density of roads and paths in the surveyed Vienna city parks is rather high and our surveys were conducted during the winter, when the majority of trees are without leaves. Hence, we think that most of the bird species could be detected and neither using path-based transects nor varying detectability of bird species was a major source of bias. All species and the number of birds heard or seen were recorded (except overflying birds), avoiding doublecounting as effectively as possible (Table S2). Waterfowl and birds with a strong affiliation to water (e.g., Grey Wagtail *Motacilla cinerea*) were excluded from further analyses as their occurrence is strongly driven by the presence of suitable waterbodies.

Quantification of avian functional diversity

Functional diversity was quantified by using four measurements. For each city park, species richness, indicating taxonomic diversity, was quantified as the total number of observed species in the survey months January 2009, December 2009, December 2012, and January 2013. Furthermore, three functional diversity metrics were used. For measuring FRic, quantifying the volume of functional trait space occupied, the convex hull volume was calculated, using the Quickhull algorithm (Barber et al. 1996; Villeger et al. 2008). Basically, this convex hull algorithm determines the most extreme trait values, links them to build the convex hull, and calculates the volume of this convex hull (Villeger et al. 2008). For calculating FEve, a minimum spanning tree is used that links all the points in a multi-dimensional trait space with the minimum sum of branch lengths (Villeger et al. 2008). Functional evenness then measures the regularity of points along this tree and the regularity in their abundances (Villeger et al. 2008). FDiv is measured using an index that quantifies how species differ in their distances (weighted by their abundances) from the center of gravity in the functional space (Villeger et al. 2008).

For calculating functional diversity indices, a trait matrix was built. Twenty functional traits were selected, which are commonly used in functional diversity research of bird communities (Petchey et al. 2007; Flynn et al. 2009; Ding et al. 2013), describing how organisms acquire resources from their environment and reflecting resource use requirements (Tables 1, S3). Data on the trait categories foraging substrate, foraging method, and diet were extracted from faunal monographs (Glutz von Blotzheim 1985–1999). Data on body mass were extracted from Dunning (2008). The functional diversity metrics were calculated in R 2.15.1 (R Core Team 2012), using the function dbFD of the FD package (Laliberte and Legendre 2010; Laliberte and Shipley 2011).

Table 1. Functional traits used for calculating functional diversity indices of wintering bird communities in Vienna city parks.

Trait category	Trait	Type of variable	Range or short description of categories
Resource quantity	Body mass [g]	Continuous	6.8 – 1246.8
Foraging substrate	Ground	Categorical	0 = not used
	Foliage		1 = rarely used
	Bark		2 = moderately used
	Air		3 = often used
Foraging method	Gleaning	Categorical	0 = not used
	Pecking		1 = rarely used
	Hawking		2 = moderately used
	Sally		3 = often used
	Probing		
Diet	Mammals	Categorical	
	Fishes		
	Amphibians, Reptiles		
	Birds		0 = not used
	Carrion		1 = rarely used
	Arthropods		2 = moderately used
	Annelids		3 = often used
	Snails		
	Fruits		
	Seeds		

Statistical analysis

Due to strong multicollinearity of urban landscape variables, we selected the variable sealed area as proxy for landscape permeability (Table S4). An increasing fraction of sealed areas proved to negatively affect bird species richness in urban areas (Fontana et al. 2011). Multiple linear regressions were carried out to describe relationships between city park variables and taxonomical and functional diversity measures of bird communities. In advance, park size was log-transformed ($\log x + 1$) to improve the fit to normality. Models were fitted using all predictor variables and possible subsets. To identify predictor variables with the strongest influence on the response variables, models were ranked according to their information content determined by the Akaike's information criterion corrected for small-sample bias (AIC_c) as the sample size divided by the number of parameters included in the models was < 40 (Symonds and Moussalli 2011). Best models, having lowest AIC_c values and thus highest Akaike weights (as the relative likelihood of the model being the best), were considered to have the best fit with the data. Models that had an AIC_c difference (Δ_i) < 2 from the best model were considered to be "best ranked." To describe the effects of the variables that affected the functional diversity measures after controlling for other variables, β coefficients were used. Furthermore, predicted relationships between avian diversity measures and the park characteristics included in the models with the lowest AIC_c value were plotted. All statistical analyses were carried out using the R packages AICcmodavg, rms, and QuantPsys.

Results

Park size was included in four of the six best ranked models of taxonomical and functional diversity metrics and positively affected species richness, FRic, and FDiv (Fig. 2, Table 2). Sealed area was part of the best ranked models for species richness and FDiv and had strong negative effects on these two bird metrics (Fig. 2, Table 2). Canopy heterogeneity was not included in models with lowest AIC_c, but played a minor role in the best ranked models of FDiv (Table 2). None of the three predictor variables park size, sealed area, and canopy heterogeneity achieved a significant model fitting for the response variable FEve.

Table 2. Best ranked models ($\Delta_i < 2$) for the bird metrics No. Spec. (species richness), FRic (functional richness), and FDiv (functional divergence). For all included variables, β coefficients are provided. Furthermore, number of estimable parameters (K), Akaike's information criterion corrected for small-sample bias (AIC_c), differences in AIC_c values of each model compared with the model with the lowest AIC_c value (Δ_i), and the Akaike weights (ω_i) are listed.

	No. Spec.	FRic	FDiv			
	1.	1.	1.	2.	3.	4.
Variables included						
Park size	0.85	0.75	0.27		0.23	
Sealed area	-0.18		-0.43	-0.45	-0.39	-0.52
Canopy heterogeneity				-0.25	-0.21	
Model summary						
K	4	3	4	4	5	3
AIC _c	183.10	415.04	-50.13	-49.71	-49.51	-49.36
Δ_i	0.00	0.00	0.00	0.42	0.62	0.76
ω_i	0.68	0.61	0.29	0.24	0.21	0.20
R^2	0.85	0.56	0.33	0.32	0.37	0.27
<i>adjusted R</i> ²	0.84	0.54	0.29	0.28	0.31	0.24

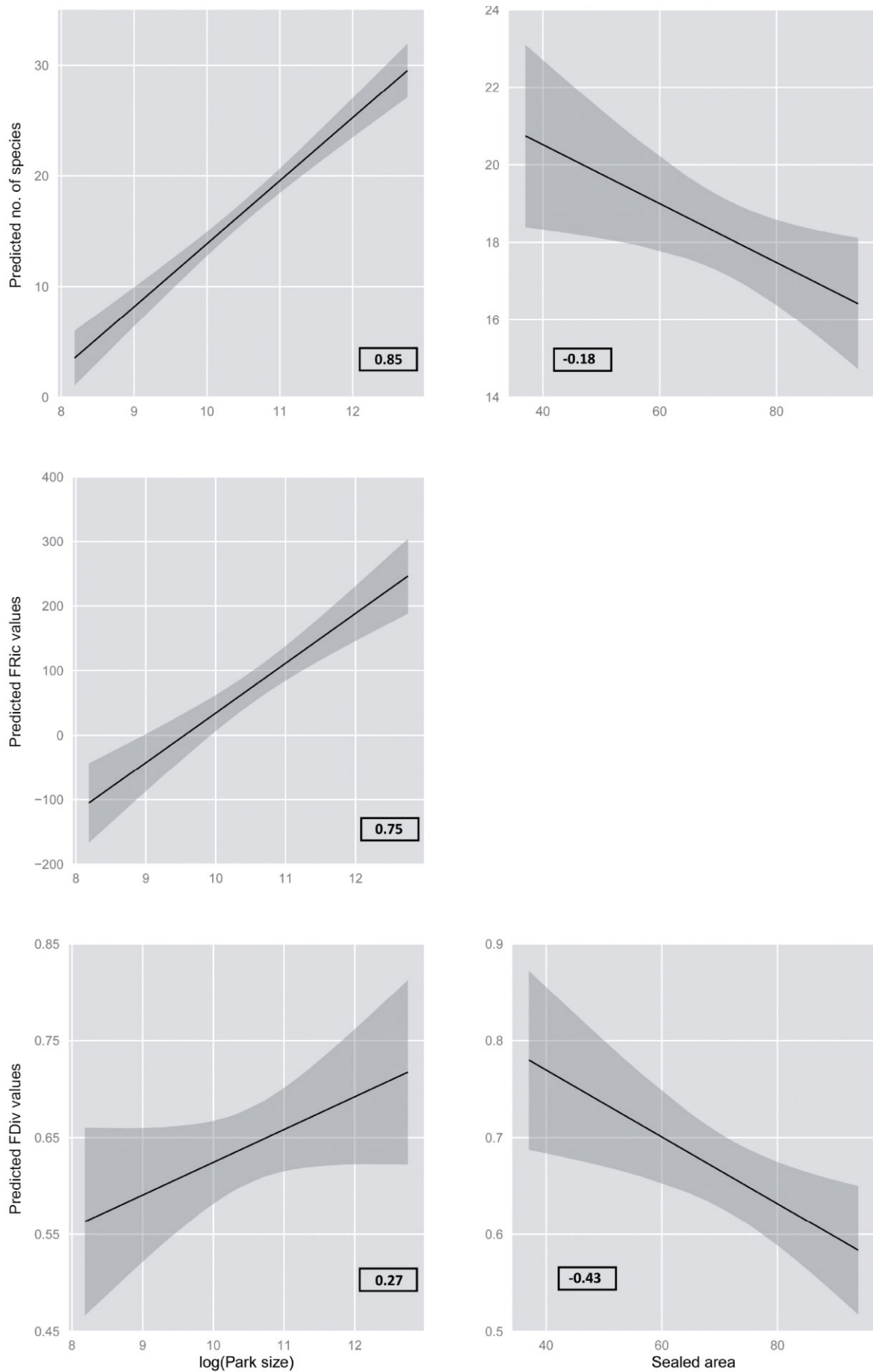


Figure 2. Predicted relationships between the two city park characteristics park size (ha) and proportion of sealed area (%) included in the model with the lowest AIC_c value and no. of species (taxonomic diversity), FRic (functional richness), and FDiv (functional divergence). Correlation coefficients (β coefficients) of each relationship are listed in the graphs.

Discussion

Park size

Park size is a very important parameter in explaining differences between city parks in the considered taxonomic and functional diversity metrics, as it was included in the best ranked models for species richness, FRic, and FDiv. As in other studies, park size strongly positively affected species richness (e.g., Jokimäki 1999; Fernández-Juricic 2000a; Fernández-Juricic and Jokimäki 2001; Murgui 2007). Even in very small urban green spaces, ranging from 0.1 to 2 ha in size, the area of green space was the most important variable positively influencing bird species richness in the city of Pachuca, Mexico (Carbó-Ramírez and Zuria 2011). This positive species–area relationship also follows the predictions of the theory of island biogeography (MacArthur and Wilson 1967), which is often applied in the study of urban bird communities as urban parks represent remnant habitat patches being isolated from the surrounding urban matrix and therefore representing the only refuges for many bird species (Davis and Glick 1978; Fernández-Juricic and Jokimäki 2001). Higher species numbers in larger parks may partly be explained by an increase in habitat complexity and resource availability in larger parks compared to smaller ones (Fernández-Juricic and Jokimäki 2001; Cornelis and Hermy 2004). Hence, the specific requirements of certain forest or insectivorous bird species will be only met in larger habitat fragments (Fernández-Juricic 2000a; Zarette et al. 2000). Furthermore, large city parks – as remnants of seminatural green space embedded in an urban landscape – have larger core areas that are unaffected by effects associated with habitat edges, such as microclimatic differences, a higher predation risk, or higher levels of human disturbances (Saunders et al. 1991; Fernández-Juricic 2001; Schneider et al. 2012). Therefore, in large parks beside edge specialist species, being highly habituated to human activities and showing high breeding densities at urban park edges, also species with specific habitat requirements can be found in the more undisturbed core areas (Fernández-Juricic 2001).

Because of a greater habitat complexity and more prominent core areas in larger parks, increasing park size results not only in a higher number of recorded species, but also in an increase in FRic as larger niche space can be filled by avian communities. This is consistent with the results of a study on bird communities of land-bridge islands in the Thousand Island Lake, China, where FRic was positively related to island area (Ding et al. 2013).

Park area was also positively related to FDiv, what may indicate a relaxation of environmental filters as emphasized for fish assemblages (Teresa and Casatti 2012). As FDiv increases with park size, bird communities in small parks show a functionally more concentrated distribution of species within functional space compared to communities of larger city parks (Mason et al. 2005). Small city parks have higher perimeter–core ratios than large ones, making them more open to edge effects associated with the urban matrix, such as higher levels of car and pedestrian traffic (Fernández-Juricic 2001). As a consequence, the environmental filtering due to urbanization may be enhanced, limiting the occurrence of high trait diversity and resulting in highly similar communities (Teresa and Casatti 2012). These communities may mainly consist of urban exploiters, which are highly adapted to urban environments, as they are dependent on human resources and are independent of amount and structure of vegetation (Blair 2001; McKinney 2008). In contrast, large habitat patches are characterized by an increase in habitat complexity and availability of resources such as food and nest sites (Saunders et al. 1991; Cornelis and Hermy 2004; Sitompul et al. 2004). Therefore, large city parks provide a large diversity of habitats necessary to support many species with different habitat requirements (Fernández-Juricic and Jokimäki 2001).

Sealed area

In accordance with other studies on bird communities of urban green spaces, the increasing urbanization degree of the surrounding landscape negatively affected species richness of city parks (Carbó-Ramírez and Zuria 2011; Ikin et al. 2013). Forest bird species moving through fragmented landscapes are strongly limited by the degree of patch connectivity, quantified by the presence of corridors or the distance between patches (Norris and Stutchbury 2001; Uezu et al. 2005). As urban bird populations in city parks can be seen as sets of semi-independent populations embedded in an inhospitable urban matrix connected by dispersal to themselves and to regional populations (Fernández-Juricic 2004), they may also be affected by the permeability of the urban matrix. Therefore, an increase in urbanization degree reduces the permeability of the urban landscape due to longer distances between remnant habitat patches and lower number of corridors such as wooded streets, both exerting a positive influence on the connectivity between city parks (Fernández-Juricic 2000b; Husté and Boulonier 2011). As a consequence, the dispersal abilities of habitat specialist species, reluctant to move through unsuitable urban matrix, may decrease, reducing the chances of park occupation and therefore local bird diversity (Fernández-Juricic 2000a).

These decreasing dispersal abilities of habitat specialist species may also cause lower FDiv values of avian communities, indicating that city parks surrounded by high proportion of sealed area harbor bird species which are functionally more similar to each other (Teresa and Casatti 2012).

Canopy heterogeneity

The extent of the tree layer within a city park is, especially for specialist bird species, of high importance as it provides nesting habitat, food resources, and refuge from predators and human disturbance (Murgui 2007). Consequently, bird species richness in urban areas is correlated with tree density (Sandström et al. 2006). A decrease in closed forest cover confronts birds with a higher degree of edge habitats and the negative effects linked to it, such as an increase in predation risk or human disturbance (Fernández-Juricic 2001; Schneider et al. 2012). In contrast to other studies, showing effects of forest edges on the considered bird responses (Barbaro et al. 2014), canopy heterogeneity played a minor role in explaining the taxonomical and functional diversity indices, as it was not included in the models with the lowest AIC_c values.

Conclusion

Surprisingly, FEve did not respond to changes in park characteristics, although it proved to be sensitive to environmental filtering in simulated communities (Mouchet et al. 2010). Also empirical data showed that FEve was negatively affected by habitat fragmentation and environmental gradients of disturbance, respectively (Filippi-Codaccioni et al. 2009; Pakeman 2011; Ding et al. 2013). In contrast, the declines of FRic and FDiv provide strong evidence for a loss of functional diversity from small toward large city parks. This indicates that bird assemblages of parks embedded in an urban landscape matrix with a high permeability for forest birds (due to a high density of green spaces) most likely provide an increased ecosystem function. These results have important implications for urban planning aiming to promote and maintain high diversity and ecosystem function in modern human-dominated landscapes.

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Conflict of Interest

None declared.

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Supporting Information

Table S1: Habitat characteristics of 36 Vienna city parks, where winter bird surveys were conducted. Beside park size and canopy heterogeneity, also the area of each habitat parameter describing the urban landscape matrix in a circle of radius 500 m around the centroid of each city park are presented. Landscape measures used for analyses are shaded in grey. Also calculation of canopy heterogeneity and proportion of sealed area is indicated.

(V1) City park code	(V2) Urban park	(V3) Area (ha)	(V4) Canopy edge length (m)	(V5) Closed canopy area (m ²)	(V6) Canopy heterogeneity (m/m ²) [= V4/V5]	(V7) Natural green space (m ²)	(V8) Man-made green space (m ²)	(V9) Forest (m ²)	(V10) Sealed area (m ²)	(V11) Proportion of sealed area [=V10/(V7+V8+V9+V10)]
01	Alfred Böhm Park	2.8	1204.06	17816.80	0.068	30961.70	206679.72	0.00	490564.12	0.67
02	Alfred-Grünwald-Park	0.8	694.60	3149.60	0.221	0.00	58616.13	0.00	714901.05	0.92
03	Allerheiligenpark	2.1	1257.11	13595.00	0.092	43215.60	97159.12	0.00	540368.86	0.79
04	Alois Drasche Park	2.0	1471.30	12709.70	0.116	3.97	99267.47	0.00	596500.12	0.86
05	Arenbergpark	2.9	1670.61	15744.50	0.106	193.40	122001.92	0.00	619418.00	0.84
06	Auerwelsbachpark	14.2	10250.50	63300.70	0.162	39433.00	130396.24	0.00	413268.25	0.71
07	Augarten	34.5	20239.70	186473.00	0.109	17663.00	89770.62	0.00	320874.03	0.75
08	Börsepark	0.4	248.59	2622.71	0.095	0.00	45564.42	0.00	711327.13	0.94
09	Botanischer Garten	9.6	4791.21	52391.10	0.091	73450.00	109615.97	0.00	479202.65	0.72
10	Burggarten	2.9	1787.13	10538.90	0.170	0.00	89294.07	0.00	659930.98	0.88
11	Casinopark Baumgarten	4.3	2572.62	17952.20	0.143	27008.00	289974.23	0.00	355918.74	0.53
12	Esterhazypark	1.0	979.30	5289.63	0.185	2086.47	62416.08	0.00	704840.25	0.92
13	Fridtjof-Nansen-Park	6.6	3838.70	26215.40	0.146	18416.30	324555.18	0.00	345180.16	0.50
14	Friedhof St. Marx	6.7	1234.78	60226.60	0.021	30830.43	157479.61	174.40	479679.01	0.72
15	Grete Rehor Park	0.7	627.37	3427.20	0.183	0.00	133840.15	0.00	632979.64	0.83
16	Haydnpark	2.1	787.05	11662.90	0.067	26517.10	97188.90	0.00	595374.13	0.83
17	Heiligenstädterpark	8.0	4340.36	53221.70	0.082	2024.40	361010.63	0.00	310188.23	0.46
18	Hugo-Wolf-Park	5.9	2992.76	40171.00	0.075	45445.40	239877.88	27573.90	404195.12	0.56
19	Kongresspark	4.6	3304.66	23434.40	0.141	0.00	188660.10	0.00	517416.36	0.73
20	Liechtensteinpark	4.8	2236.28	23095.00	0.097	0.00	94885.86	0.00	629103.70	0.87
21	Napoleonwald	3.1	1885.16	19762.80	0.095	4210.90	459655.10	0.00	272321.42	0.37
22	Ölzeltpark	1.1	569.92	7755.72	0.073	11179.07	408339.13	19605.80	326488.13	0.43
23	Ostarrichipark	1.1	308.92	2342.54	0.132	0.00	126929.19	0.00	638491.98	0.83
24	Park der Universitätssternwarte	5.8	631.57	52134.10	0.012	8400.50	159671.00	0.30	520933.09	0.76
25	Penzinger Friedhof	4.5	2750.19	26800.90	0.103	0.00	94939.66	0.00	634550.59	0.87
26	Rathauspark	4.5	2558.90	27561.30	0.093	23738.00	126517.95	0.00	313726.34	0.68
27	Schweizergarten	15.9	8266.24	81700.50	0.101	0.00	50220.17	0.00	565850.96	0.92
28	Stadtpark	13.4	7929.05	63392.00	0.125	13218.40	122195.24	0.00	631507.62	0.82
29	Steinbauerpark	1.1	446.29	5153.12	0.087	92531.50	220609.20	51955.60	395035.73	0.52
30	Türkenschanzpark	15.5	10301.30	95932.00	0.107	23045.00	231694.13	57979.66	313604.69	0.50
31	Vogelweidpark	1.8	1138.59	7495.30	0.152	0.00	86557.49	0.00	671276.98	0.89
32	Volksplatz	19.2	10226.30	100487.00	0.102	78971.00	256822.15	1331.06	246802.22	0.42
33	Währingerpark	6.8	4216.33	33891.60	0.124	18892.50	197568.81	0.00	488160.01	0.69
34	Waldmüllerpark	4.4	2215.72	30833.10	0.072	0.00	78664.11	15874.10	559790.28	0.86
35	Wertheimsteinpark	6.8	4443.41	44196.50	0.101	18457.20	210613.88	332.51	417508.81	0.65
36	Wilhelmsdorfer Park	2.2	1298.82	9591.59	0.135	0.00	128424.60	5289.31	555194.28	0.81

Table S2. Total number of individuals of bird species recorded in 36 city parks in Vienna. City park codes in the columns refer to Table S1.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Accipiter nisus</i>	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0
<i>Aegithalos caudatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	23	0	0	4	0
<i>Bombycilla garrulus</i>	230	0	0	0	0	0	11	0	0	0	0	0	130	0	0	0	30	0
<i>Buteo buteo</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carduelis carduelis</i>	0	0	1	51	19	0	16	11	16	0	1	0	55	0	0	0	9	0
<i>Carduelis spinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Certhia brachydactyla</i>	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	1
<i>Certhia familiaris</i>	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0
<i>Chloris chloris</i>	0	2	0	6	30	25	148	1	27	5	40	1	42	40	0	0	3	10
<i>Coccothraustes coccothraustes</i>	2	0	0	0	0	3	6	0	1	0	7	0	9	0	0	0	33	6
<i>Columba livia f. domestica</i>	58	20	444	157	192	132	808	45	10	132	0	201	3	6	158	106	12	0
<i>Columba palumbus</i>	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	9	2
<i>Corvus corone</i>	16	0	8	21	106	141	516	0	66	42	12	5	10	9	8	10	95	28
<i>Corvus frugilegus</i>	156	1	5	58	163	156	207	0	55	36	62	4	304	46	41	37	115	269
<i>Corvus monedula</i>	0	0	0	0	0	0	23	0	0	0	0	0	0	0	0	0	0	0
<i>Cyanistes caeruleus</i>	24	7	7	19	31	61	101	0	43	14	12	4	13	34	1	7	38	14
<i>Dendrocopos major</i>	6	0	2	2	6	14	36	0	7	3	10	1	2	4	1	1	12	6
<i>Dendrocopos medius</i>	0	0	1	0	0	1	5	0	2	2	1	0	0	0	0	0	1	0
<i>Emberiza citrinella</i>	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0
<i>Erithacus rubecula</i>	1	1	1	1	0	1	3	0	7	1	1	0	4	5	0	0	8	1
<i>Falco peregrinus</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Falco tinnunculus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Fringilla coelebs</i>	5	0	0	0	3	25	33	0	10	5	24	0	12	88	0	0	25	2
<i>Fringilla montifringilla</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1
<i>Garrulus glandarius</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
<i>Lophophanes cristatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	1
<i>Nucifraga caryocatactes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Parus major</i>	103	41	31	58	103	201	642	12	169	74	74	23	81	140	9	48	231	64
<i>Passer domesticus</i>	0	70	5	0	5	1	19	0	0	0	13	4	46	0	0	0	3	0
<i>Passer montanus</i>	0	0	0	0	0	43	53	0	0	0	0	0	0	0	0	0	0	0
<i>Periparus ater</i>	0	0	0	0	0	3	0	0	3	0	6	0	5	4	0	1	2	0
<i>Phoenicurus ochruros</i>	0	0	0	0	0	0	9	0	0	1	0	0	0	0	0	0	0	0
<i>Pica pica</i>	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
<i>Picus viridis</i>	0	0	0	0	0	3	8	0	2	0	1	0	0	0	0	0	1	0
<i>Poecile palustris</i>	0	0	0	0	0	4	0	0	2	0	5	0	0	25	0	0	9	0
<i>Psittacula krameri</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Pyrrhula pyrrhula</i>	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	1	0
<i>Regulus regulus</i>	0	0	0	0	0	1	0	0	16	2	6	0	17	15	0	0	4	23
<i>Sitta europaea</i>	2	0	2	6	7	43	47	2	19	12	14	0	4	0	0	0	25	8
<i>Streptopelia decaocto</i>	0	0	0	0	2	0	2	0	0	0	0	0	16	0	0	0	0	0
<i>Troglodytes troglodytes</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
<i>Turdus iliacus</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	44	14
<i>Turdus merula</i>	23	16	4	5	19	22	144	16	64	29	16	2	12	58	6	9	45	14
<i>Turdus philomelos</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Turdus pilaris</i>	0	0	0	0	0	0	3	0	0	0	0	0	1	9	0	0	1	0
<i>Turdus viscivorus</i>	0	0	0	0	0	3	2	1	1	0	0	0	0	1	0	0	5	2

Table S2 (continued). Total number of individuals of bird species recorded in 36 city parks in Vienna. City park codes in the columns refer to Table S1.

Species	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
<i>Accipiter nisus</i>	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	2	0
<i>Aegithalos caudatus</i>	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bombycilla garrulus</i>	0	0	0	0	0	0	40	9	194	0	0	124	0	1	380	0	60	0
<i>Buteo buteo</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Carduelis carduelis</i>	10	44	15	22	0	0	5	5	4	11	1	12	5	22	0	1	0	12
<i>Carduelis spinus</i>	0	0	1	0	0	0	1	0	1	1	0	5	0	1	0	0	0	0
<i>Certhia brachydactyla</i>	0	0	2	0	0	1	3	0	4	0	0	2	0	1	0	0	2	0
<i>Certhia familiaris</i>	0	0	0	0	0	0	2	0	8	0	0	3	0	3	0	0	0	0
<i>Chloris chloris</i>	36	3	29	1	0	9	18	30	102	83	1	9	6	31	12	14	5	1
<i>Coccothraustes coccothraustes</i>	13	0	6	4	0	17	2	0	32	11	0	26	0	1	5	16	14	0
<i>Columba livia f. domestica</i>	91	1	0	0	23	0	121	111	962	572	401	102	47	29	48	87	50	457
<i>Columba palumbus</i>	0	0	30	0	0	0	0	0	0	0	0	9	0	1	0	0	0	0
<i>Corvus corone</i>	62	31	14	0	2	19	6	23	153	141	4	235	2	106	79	2	11	4
<i>Corvus frugilegus</i>	121	3	100	236	24	0	273	42	240	84	3	477	2	484	144	140	27	18
<i>Corvus monedula</i>	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
<i>Cyanistes caeruleus</i>	23	27	11	8	1	48	32	14	33	86	6	55	4	62	36	30	29	4
<i>Dendrocopos major</i>	6	11	10	2	0	12	11	1	14	18	0	23	0	18	6	3	10	3
<i>Dendrocopos medius</i>	0	1	1	0	0	1	1	1	3	1	0	6	0	3	2	0	0	0
<i>Emberiza citrinella</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Erithacus rubecula</i>	0	1	0	0	1	1	1	1	3	4	0	6	0	0	3	0	6	0
<i>Falco peregrinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Falco tinnunculus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Fringilla coelebs</i>	20	12	4	2	0	13	16	13	13	20	0	33	0	54	19	9	15	2
<i>Fringilla montifringilla</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Garrulus glandarius</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	9	0	0	1	0
<i>Lophophanes cristatus</i>	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
<i>Nucifraga caryocatactes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Parus major</i>	118	88	26	29	7	150	110	63	143	244	8	223	28	277	81	130	146	35
<i>Passer domesticus</i>	8	0	0	0	26	0	0	7	34	32	7	0	12	0	2	1	0	188
<i>Passer montanus</i>	0	0	0	2	0	0	0	0	0	0	0	0	0	34	0	1	0	0
<i>Periparus ater</i>	1	0	0	0	0	1	2	0	1	0	0	4	0	8	0	0	1	0
<i>Phoenicurus ochruros</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pica pica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Picus viridis</i>	1	1	0	0	0	3	0	0	1	0	0	5	0	9	1	0	1	0
<i>Poecile palustris</i>	0	0	3	0	0	0	2	0	0	1	0	10	0	10	6	0	2	0
<i>Psittacula krameri</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pyrrhula pyrrhula</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	0	2	0
<i>Regulus regulus</i>	0	0	0	0	0	1	5	0	2	0	0	14	0	31	9	6	36	0
<i>Sitta europaea</i>	15	10	7	5	0	26	16	8	44	52	0	68	0	54	17	16	24	1
<i>Streptopelia decaocto</i>	1	0	2	0	0	0	6	0	0	11	0	1	0	0	0	0	0	0
<i>Troglodytes troglodytes</i>	1	0	0	0	0	2	2	0	0	2	0	3	0	0	2	0	3	0
<i>Turdus iliacus</i>	0	0	0	0	0	17	1	0	2	3	0	139	0	0	44	0	71	0
<i>Turdus merula</i>	46	56	3	5	9	33	9	51	129	164	7	77	28	46	84	43	84	20
<i>Turdus philomelos</i>	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Turdus pilaris</i>	2	0	0	1	0	1	0	0	0	0	0	10	0	0	1	0	0	0
<i>Turdus viscivorus</i>	0	0	14	0	0	14	1	0	10	0	0	16	0	4	2	0	15	0

Table S3. Biological traits of all bird species considered in this study. Foraging substrate: G – ground, F – foliage, B – bark; A – air; foraging method: Gle – gleaning¹, Pec – pecking², Haw – hawking³, Sal – sally⁴, Pro – probing⁵; diet: Bir – birds, Mam – mammals, Fis – fishes, Amp – amphibians/reptiles, Sna – snails, Art – Arthropods, Ann – Annelides, See – Seeds, Fru – Fruits, Car – Carrion. Numbers indicate the extent of usage (0 – not used to 3 – often used).

Species	Body mass [g]	Foraging substrat				Foraging method					Diet									
		G	F	B	A	Gle	Pec	Haw	Sal	Pro	Bir	Mam	Fis	Amp	Sna	Art	Ann	See	Fru	Car
<i>Accipiter nisus</i>	185.50	1	0	0	3	0	0	3	0	0	3	1	0	0	0	0	0	0	0	0
<i>Aegithalos caudatus</i>	7.70	1	3	0	1	3	2	0	1	0	0	0	0	0	0	3	0	1	1	0
<i>Bombycilla garrulus</i>	57.80	1	3	0	0	0	3	0	1	0	0	0	0	0	0	1	0	0	3	0
<i>Buteo buteo</i>	904.84	3	0	0	1	0	0	3	0	0	1	3	0	2	0	1	0	0	0	2
<i>Carduelis carduelis</i>	15.80	2	3	0	1	1	3	0	1	0	0	0	0	0	0	1	0	3	1	0
<i>Carduelis spinus</i>	14.00	0	3	0	0	0	3	0	0	0	0	0	0	0	0	1	0	3	0	0
<i>Certhia brachydactyla</i>	8.50	2	0	3	0	3	1	0	0	0	0	0	0	0	2	3	0	1	1	0
<i>Certhia familiaris</i>	8.50	1	0	3	0	3	1	0	0	0	0	0	0	0	0	3	0	2	0	0
<i>Chloris chloris</i>	30.65	3	3	0	0	0	3	0	0	0	0	0	0	0	0	1	0	3	0	0
<i>Coccothraustes coccothraustes</i>	55.40	2	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0
<i>Columba livia f. domestica</i>	347.00	3	1	0	1	0	3	0	1	0	0	0	0	0	1	1	1	3	1	0
<i>Columba palumbus</i>	488.00	2	3	0	0	0	3	0	0	0	0	0	1	0	1	1	1	3	2	0
<i>Corvus corone</i>	558.74	3	2	0	0	0	3	0	0	2	0	2	0	2	2	2	2	3	2	2
<i>Corvus frugilegus</i>	485.70	3	1	0	1	0	2	0	0	3	0	1	0	0	1	1	1	3	2	2
<i>Corvus monedula</i>	244.35	3	1	0	2	0	3	0	0	1	0	1	0	0	1	1	1	3	2	2
<i>Cyanistes caeruleus</i>	10.73	1	3	0	1	2	3	0	1	0	0	0	0	0	0	2	0	3	2	0
<i>Dendrocopos major</i>	75.55	1	2	3	0	2	3	0	0	1	0	1	0	0	0	2	1	3	1	1
<i>Dendrocopos medius</i>	59.00	1	2	3	0	1	2	0	0	3	0	0	0	0	0	2	0	3	1	0
<i>Emberiza citrinella</i>	29.80	3	3	0	1	0	3	1	0	0	0	0	0	0	1	1	0	3	0	0
<i>Erithacus rubecula</i>	17.97	3	2	0	1	1	3	0	1	0	0	0	3	3	3	3	3	3	2	0
<i>Falco peregrinus</i>	697.50	0	0	0	3	0	1	3	0	0	3	1	0	1	0	1	0	0	0	1
<i>Falco tinnunculus</i>	209.00	3	0	0	2	0	1	3	1	0	3	2	1	1	0	1	1	0	1	1
<i>Fringilla coelebs</i>	23.60	3	2	0	1	0	3	0	1	0	0	0	0	0	0	1	0	3	0	0
<i>Fringilla montifringilla</i>	30.25	3	1	0	0	0	3	0	1	0	0	0	0	0	1	2	0	3	0	0
<i>Garrulus glandarius</i>	175.00	1	3	1	0	0	3	0	0	2	0	3	0	0	1	1	0	1	3	1
<i>Lophophanes cristatus</i>	11.14	2	3	0	1	3	2	0	1	0	0	0	0	0	0	3	0	2	1	0
<i>Nucifraga caryocatactes</i>	162.35	2	3	2	0	0	3	0	0	2	1	1	0	0	0	1	0	3	2	1
<i>Parus major</i>	19.11	3	2	0	1	2	3	0	1	0	1	0	0	0	1	2	0	3	1	0
<i>Passer domesticus</i>	30.40	3	1	0	1	2	3	0	1	0	0	0	1	1	1	1	0	3	1	1
<i>Passer montanus</i>	23.00	3	2	0	1	2	3	0	1	0	0	0	0	0	0	2	0	3	1	0
<i>Periparus ater</i>	8.98	1	3	1	0	1	3	0	0	1	0	0	0	0	0	2	0	3	0	0
<i>Phoenicurus ochruros</i>	17.30	3	0	0	2	1	3	0	2	0	0	0	0	0	0	3	0	0	2	0
<i>Pica pica</i>	206.10	3	1	0	1	0	3	0	1	2	0	3	0	0	2	3	2	2	2	0
<i>Picus viridis</i>	176.00	3	0	1	0	1	3	0	0	3	0	0	0	1	1	3	1	1	2	0
<i>Poecile palustris</i>	11.00	1	3	0	1	2	3	0	1	0	0	0	0	0	0	2	0	3	1	0
<i>Psittacula krameri</i>	148.75	3	1	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	2	0
<i>Pyrrhula pyrrhula</i>	32.95	2	3	0	1	0	3	0	1	0	0	0	0	0	0	1	0	3	1	0
<i>Regulus regulus</i>	6.80	1	3	0	1	3	0	0	1	1	0	0	0	0	0	3	0	0	0	0
<i>Sitta europaea</i>	23.10	1	2	3	1	1	3	0	1	1	0	0	0	0	0	2	0	3	1	0
<i>Streptopelia decaocto</i>	210.50	3	0	0	1	0	3	0	1	0	0	0	0	0	1	1	0	3	2	0
<i>Troglodytes troglodytes</i>	8.74	3	1	0	0	3	2	0	0	3	0	0	0	0	0	3	1	1	1	0
<i>Turdus iliacus</i>	72.80	1	3	0	0	3	2	0	0	0	0	0	0	0	1	1	1	0	3	0
<i>Turdus merula</i>	83.35	3	0	0	1	2	3	0	1	1	0	0	1	1	1	2	2	3	2	0
<i>Turdus philomelos</i>	70.00	3	0	0	0	2	3	0	0	1	0	0	0	0	2	2	2	1	3	0
<i>Turdus pilaris</i>	103.05	2	3	0	0	3	2	0	0	1	0	0	0	0	1	1	1	1	3	0
<i>Turdus viscivorus</i>	109.40	2	3	0	0	3	2	0	0	1	0	0	0	0	1	1	2	1	3	0

¹ picking food items from a substrate without manipulation of the surface; ² removing some of the exterior of the substrate by using the bill; ³ attacking in continuous flight; ⁴ flying from a perch to attack a food item and then return to the perch; ⁵ inserting the bill in holes of a firm substrate or directly into softer substrate to capture hidden food

Table S4. Correlation coefficients of Pearson correlations including the park variables park area (log transformed) and canopy heterogeneity as well as the landscape variables natural green space, man-made green space, forest and sealed area, describing the urban matrix surrounding each city park, are listed. Significant correlations ($p < 0.05$) are printed in bold.

	Park area (m ²)	Canopy heterogeneity (m/m ²)	Natural green space (m ²)	Man-made green space (m ²)	Sealed area (m ²)	Forest (m ²)
Park area (m ²)	1.00	-0.26	0.27	0.14	-0.54	0.01
Canopy heterogeneity (m/m ²)	-0.26	1.00	-0.28	-0.22	0.34	-0.18
Natural green space (m ²)	0.27	-0.28	1.00	0.20	-0.50	0.39
Man-made green space (m ²)	0.14	-0.22	0.20	1.00	-0.76	0.25
Sealed area (m ²)	-0.54	0.34	-0.50	-0.76	1.00	-0.32
Forest (m ²)	0.01	-0.18	0.39	0.25	-0.32	1.00

2.2. Local quality versus regional connectivity – habitat requirements of wintering woodpeckers in urban green spaces

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Abstract

In urban landscapes, city parks represent strongholds of avian biodiversity. Hence, understanding which variables promote species richness of bird communities has major implications for urban planning in order to sustain high biodiversity in an increasingly urbanised environment. From a management perspective, three options are available: increase park area, increase habitat quality within parks and increase connectivity between parks. We used two woodpecker species, a generalist species (Great Spotted Woodpecker) and a habitat specialist (Middle Spotted Woodpecker), as indicators to identify key variables promoting biodiversity in the city parks of Vienna. Bird surveys were carried out during winter time between 2005 and 2015 in 29 urban parks. An information theoretic approach based on generalised linear models identified park area as the most relevant local variable, positively affecting the occurrence of both species. The variable was included in all best ranked models of the two woodpecker species (based on Akaike's information criterion corrected for small-sample sizes). Other local scale variables as well as the position of city parks within the urban matrix and their connectivity were of minor importance. Our results also provide some evidence that city parks may act as refuges for birds during cold winters. The park occupancy of the Great Spotted Woodpecker increased significantly with decreasing mean winter temperatures. The management of existing parks and the planning of new parks represent opportunities to improve the ecological conditions for nature development in addition to their principal function to provide recreational, cultural and aesthetic values.

Keywords

Oak trees, urban parks, woodpeckers, urban development

Own contribution

Study design: 50 %, data collection: 30 %, statistical analyses: 80 %, manuscript preparation: 70 %

Introduction

Parks belong to the green infrastructure of cities and provide a broad range of ecological and socio-economic goods and services such as air filtration, micro-climate regulation, noise reduction, and recreational, cultural and aesthetic values (Forman 2014). Within urbanised areas, parks are also hotspots of biodiversity (Fernández-Juricic and Jokimäki 2001; Strohbach, Lerman, and Warren 2013). Understanding which variables promote biodiversity in urban parks is crucial and a prerequisite for an adequate management focused on biodiversity persistence. Hence, it is important to identify key variables sustaining biodiversity and thereby derive management recommendations for park authorities. As species richness of woodpeckers and forest bird richness are often positively related at a local scale and at a landscape level (Mikusiński, Gromadzki, and Chylarecki 2001; Roberge and Angelstam 2006; Drever et al. 2008), we used woodpeckers to identify key variables associated with their occurrence in urban parks.

Although the general importance of woodpeckers as primary cavity producers for cavity-using vertebrates may have been overrated in the past, at least in Europe where most of the tree cavities in forests are created by fungal decay and mechanical damage (e.g. by wind) (Cockle, Martin, and Wesołowski 2011), the situation may be different in urban areas. Especially in managed city parks the formation of cavities through processes such as damage or decay may be limited, as parkland is dominated by mostly healthy trees to ensure safe visits for the public (Sandström, Angelstam, and Mikusiński 2006; Aronson 2017). Hence, woodpeckers may then provide a critical resource for obligate and facultative cavity-using species, underlining their high ecological value (Paine 1969; Bonar 2000; Boonman 2000; Martin, Aitken, and Wiebe 2004). Moreover, woodpeckers are specifically sensible to increasing urbanisation (Sandström, Angelstam, and Mikusiński 2006; Myczko et al. 2014), thus management measures should early and significantly affect their occurrence. Furthermore, with their colourful plumage, distinctive vocalisations and their habit of drumming on wood and other surfaces, they are easily identifiable by the general public (Del Hoyo, Elliott, and Sargatal 2002). Consequently, these charismatic birds can easily be used to facilitate discussions about conservation of biodiversity and the importance of urban parks.

Biodiversity may be governed by local and regional factors. Urban bird ecology often focuses on the local scale, and park area was often found to be the most influential variable for the occurrence of species (Fernández-Juricic and Jokimäki 2001). Additionally, within urban green spaces variables related to vegetation, such as tree cover and tree species richness, were found to influence abundance and diversity of birds in general (Xie et al. 2016) and of woodpeckers in particular (Morrison and Chapman 2005; Sandström, Angelstam, and Mikusiński 2006; Drever et al. 2008; Myczko et al. 2014). Recently, the focus of studies of urban bird ecology has shifted to the landscape scale, but the influence of factors such as landscape connectivity on bird abundance and biodiversity is still not sufficiently understood. Some studies have shown that local variables were more important than landscape variables in determining bird diversity and abundance in highly urbanised areas (Evans, Newson, and Gaston 2009; Shwartz, Shirley, and Kark 2013). While others have found that local urban bird richness strongly depended on landscape connectivity (Loss, Ruiz, and Brawn 2009; Shanahan et al. 2011). One reason for these contradictions may lie in the often used ‘urban–rural gradient’ approach. Although being intuitive, easily measurable and practical, its interpretation is often ambiguous with regard to the underlying specific features of the urbanised areas (Beninde et al. 2015).

Generally, the importance of local versus regional variables depends on the spatial scale, the connectivity variables considered and on the traits of the species studied. Concepts of connectivity differ theoretically (e.g. patch-corridor-matrix model, graph theory), and have thus different assumptions and requirements. The patch-corridor-matrix model for instance emphasises connections via cor-

ridors, whereas graph theory stresses the position of a patch in a network. Considering species traits, it has been shown for aquatic and terrestrial invertebrates, algae and plants, that generalists are governed more by regional variables than specialist species and that dispersal ability is of crucial importance (Pandit, Kolasa, and Cottenie 2009; Dapporto and Dennis 2013; Funk, Schiemer, and Reckendorfer 2013).

We investigated the importance of local and regional scale variables on the park occupancy of two woodpecker species, the Great Spotted Woodpecker *Dendrocopos major* – one of the more generalist woodpecker species – and the Middle Spotted Woodpecker *Dendrocopos medius* – a habitat specialist (Mikusiński and Angelstam 1997). We expect that for the Middle Spotted Woodpecker park features (habitat quality) are more important than for the Great Spotted Woodpecker. In contrast, park occupancy of this habitat generalist may depend more strongly on regional variables (connectivity of parks). To our knowledge until now studies testing for effects of habitat variables on the presence and diversity of woodpecker species in urban landscapes only considered conditions during the breeding season (e.g. Morrison and Chapman 2005; Sandström, Angelstam, and Mikusiński 2006; Myczko et al. 2014). As we carried out winter surveys of woodpeckers over several years, we are able to test for differences in park occupancy between winters. During winter time densities of birds can increase in urban residential areas (Tryjanowski et al. 2015), providing some evidence of population shifts from rural towards urban areas in response to harsh weather conditions. By dispersing to urban landscapes, woodpeckers may find sufficient food supply even under adverse conditions due to supplementary feeding (Tryjanowski et al. 2015). Furthermore, they face reduced thermoregulatory stress during long, cold winter nights because of the urban heat island phenomenon (Böhm 1998). Hence, especially during harsh winters woodpeckers may more intensely use urban areas and the probability of parks being occupied by Great and Middle Spotted Woodpeckers may increase.

Beside assessing the importance of city parks as refuges for birds during cold winters, results of this study will also contribute to our knowledge on urban bird ecology with respect to local and regional determinants and thus may help facilitating management measures.

Methods

Study area

The study was conducted in Vienna, the largest city in Austria (48°13'N, 16°22'E), with a population of 1.8 million inhabitants and an area covering 415 km² (Statistics Austria 2016). Whereas 21 % of the city area are covered by densely built-up areas, around 45 % are covered by green space such as forests, meadows, agricultural areas or city parks (Wichmann et al. 2009; MA 41 2014). Thereby, forests cover around 19 % with contiguous broadleaved forests at the northern and western outskirts of Vienna, being dominated by oak and beech trees (Wichmann et al. 2009). Large riparian forests with a highly diverse tree species composition can also be found along the river Danube (Wichmann et al. 2009). Around 4 % of Vienna are covered by city parks (MA 41 2014). Woodpecker surveys were carried out in 29 urban parks, with a mean area of 2.7 ha ranging from 0.36 ha (Börsepark) to 15.52 ha (Türkenschanzpark), and spread across the city centre of Vienna (Fig. 1 and Table 1). Beside covering a sufficient variation in park area to properly resolve the effects of this variable on woodpecker occupancy, we also chose parks in relation to their absence of connections to other remnants of greenspace via corridors. Hence, no confounding effects between connectivity via corridors and our landscape matrix connectivity measures (see below) could arise. Furthermore, for all selected parks data on their tree composition was available in the tree cadastre of Vienna (see below).

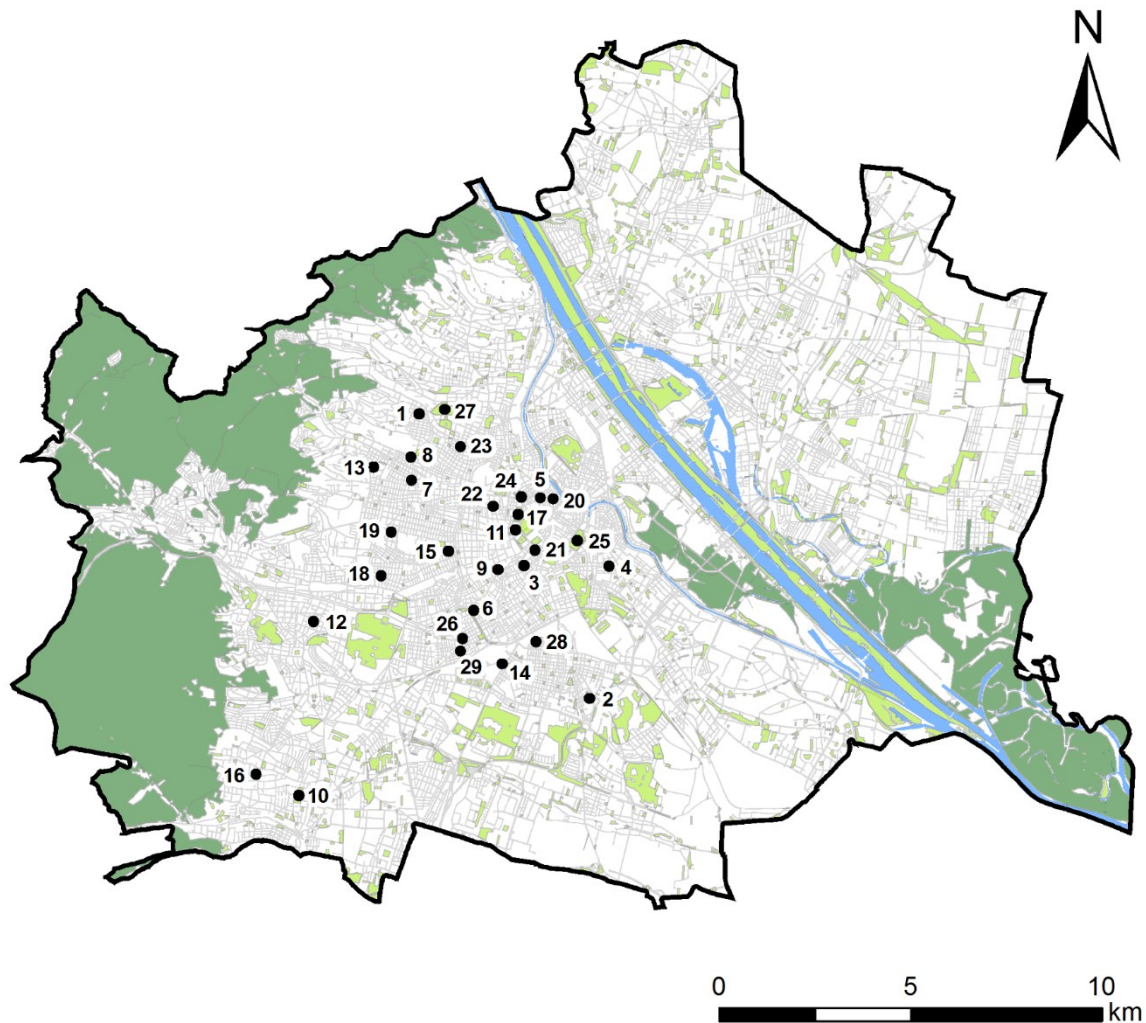


Figure 1. Map of Vienna indicating the midpoints of 29 city parks where bird surveys were carried out (black circles). City park codes refer to Table 1. Blue areas indicate the main waterbodies of the river Danube; dark green areas represent natural forests, whereas green space remnants are indicated by light green areas; light grey lines picture the road network of Vienna. The map was generated using ArcGIS 10.2 (<http://www.esri.com>, accessed 26 Mar 2016).

Weather conditions

Winter temperatures for our study area were derived from the BOKU-Met weather station (48°14'16.3"N, 16°19'53.8"E; 266 m above sea level), located northwest of the Türkenschanzpark (city park code no. 27 in Fig. 1) and operated by the University of Natural Resources and Life Sciences, Vienna (<https://meteo.boku.ac.at/wetter/mon-archiv>, accessed 19 Aug 2017). Based on a daily 10 min interval and including the months November, December and January mean winter temperatures were calculated for each winter during which bird surveys were carried out.

Table 1. List of 29 Vienna city parks, where woodpecker surveys were carried out. City park codes refer to numbers in Fig. 1. Beside park size also the presence (1) or absence (0) of the two woodpecker species Great Spotted Woodpecker (*D. major*) and Middle Spotted Woodpecker (*D. medius*) are indicated for each park. Note that the presence of a woodpecker species indicates city parks in which the species was observed at least once during surveys.

City park code	City park	Area (ha)	<i>D. major</i>	<i>D. medius</i>
1	Albert-Dub-Park	0.89	0	0
2	Alfred Böhm Park	2.76	1	0
3	Alfred-Grünwald-Park	0.81	1	0
4	Arenbergpark	2.86	1	1
5	Börsepark	0.36	0	0
6	Bruno-Kreisky-Park	1.32	0	0
7	Clemens-Hofbauer-Platz	0.59	0	0
8	Clemens-Krauss-Park	0.60	1	0
9	Esterhazypark	0.97	1	0
10	Fridtjof-Nansen-Park	6.55	1	1
11	Grete Rehor Park	0.68	1	0
12	Hügelpark	1.15	1	0
13	Kongresspark	4.59	1	1
14	Martin-Luther-King	1.98	0	0
15	Märzpark	1.58	1	0
16	Ölzelpark	1.10	1	0
17	Rathauspark	4.47	1	1
18	Reinlpark	0.55	0	0
19	Rohrauerpark	1.04	1	0
20	Rudolfspark	0.71	0	0
21	Schillerpark	0.85	0	0
22	Schönbornpark	1.05	1	0
23	Schubertpark	1.32	0	0
24	Sigmund-Freud-Park	1.47	1	0
25	Stadtpark	13.39	1	1
26	Steinbauerpark	1.13	1	0
27	Türkenschanzpark	15.52	1	1
28	Waldmüllerpark	4.38	1	0
29	Wilhelmsdorfer Park	2.20	1	1

Bird surveys

Study sites were visited four to eight times (four times: $n = 1$ city park, five times: $n = 12$, seven times: $n = 1$, eight times: $n = 15$) during winter (November – January) between 2005 and 2015 (November: 2008; December: 2005, 2009, 2012, 2013; January 2009, 2013, 2015). Thereby, 16 of the 29 city parks considered in the study were surveyed two times in the winter 2008/9 (November 2008 and January 2009) and all 29 parks were surveyed two times in winter 2012/3 (December 2012 and January 2013). Woodpeckers were surveyed between 08:00 AM and 16:00 PM under favourable weather conditions (i.e. avoiding windy days and/or days of heavy rain and snowfall). Sampling effort was standardised

according to park size (10 min/1 ha). The existing network of paths and roads within a park was used for survey routes, trying to cover the entire area of the park in a zigzag-manner. During surveys each woodpecker species heard or seen was recorded, not considering over-flying birds. To avoid the attraction of individuals from surrounding areas, we did not use playback techniques. Furthermore, during winter leafless trees in combination with the conspicuous foraging behaviour of woodpeckers as well as their characteristic calls ensure reliable survey results in the presence of woodpeckers within city parks, even without using playback techniques.

Local scale variables

For analysis, we considered park area and the number of woody plant species as they have been shown to influence bird abundance and diversity in parks (Fernández-Juricic and Jokimäki 2001; Shwartz, Shirley, and Kark 2008). Additionally, we included variables presumably important for woodpeckers such as basal area (Morrison and Chapman 2005). For Great Spotted Woodpeckers patch occupancy seems to be related to the density of large trees (> 30 cm diameter at breast height = DBH; Barrientos 2010). The density of large *Quercus* trees (≥ 37 cm DBH) represents an important habitat requisite for Middle Spotted Woodpeckers during as well as outside the breeding season (Robles et al. 2007; Domínguez, Carbonell, and Ramírez 2017; Robles and Ciudad 2017). Consequently, both variables were included in our analyses to describe local habitat quality of urban city parks.

Park area was calculated in ArcGIS 10.2 (ESRI) based on Vienna land use data from the period 2009 to 2012 (City of Vienna 2016). All other local scale variables derived from data of the tree cadastre of Vienna (date of origin: October 2011), containing information about every live tree (DBH, tree species) planted in the 29 city parks considered in the study (City of Vienna 2016). Based on these data, the amount of woody vegetation within each city park was quantified by calculating the basal area (m^2)/ha and as the proportion of total park area (%) for trees with DBH > 10 cm (Hédli et al. 2009). Furthermore, number of tree genera (as surrogate for structural diversity) as well as the density of large oaks and large trees were calculated for each park.

Regional scale variables

Regional scale variables were assessed for all 29 city parks in which bird surveys were carried out. For calculating the analysis of the spatial structure of the park network we delineated further 782 parks and other remnants of green space (meadows, lawns and woodlots) using Vienna land use data of the year 2009 (City of Vienna 2016). The mean size of these patches was 2.0 ha and ranged from 0.04 to 121 ha. To quantify connectivity measures we used network analysis (Minor and Urban 2007; Cumming 2010) where the landscape is represented as a set of nodes (points representing habitat patches or sampling sites) connected by edges between them. An edge between two nodes implies that there is some flux between those nodes, as in the case of dispersal between two patches (Minor and Urban 2007). The network was represented by a complete graph, i.e. every node (= park) was connected to each other. We used different network centrality measures to quantify the position of a park in the city (i.e. its connectivity to other urban green spaces), which allowed us to analyse connectivity at different spatial scales and with different focus. Three measures (CN_{IDW} , $\text{CN}_{\text{IDW}2}$ and $\text{CN}_{\text{IDW}3}$) focused only on the position of the parks within the network, ignoring the sizes of the areas they are connected to. Three additional measures (CA_{IDW} , $\text{CA}_{\text{IDW}2}$ and $\text{CA}_{\text{IDW}3}$) also took into account the size of patches they are connected to. We applied three methods of inverse distance weighting to allow for the analysis at different spatial scales. IDW gives a linear weight to distances, IDW2 a squared weight and IDW3 a cubic weight. That means that IDW3 has a stronger focus on the network configuration nearby the sampling site whereas IDW also takes into account patches further away. All connectivity measures were standardised $[(\text{raw value} - \text{mean})/\text{standard deviation}]$. Additionally, we also included the distance

to the nearest breeding site as wintering birds may less likely occur in city parks which are further away from their breeding habitats. This may especially be the case for the Middle Spotted Woodpecker, the most resident European woodpecker (Pettersson 1985) and occupying similar home ranges during winter and breeding period (Pasinelli 2003). As available data on the breeding distribution of the two woodpecker species are based on a 618 m x 618 m grid (Wichmann et al. 2009), we calculated the nearest distance between the centroid of each of the 29 city parks and the midpoint of the grid cell showing breeding records of the respective woodpecker species.

We also analysed the landscape matrix surrounding each park in more detail based on Vienna land use data from the period 2010 to 2012 (City of Vienna 2016). Analysis was performed at a circle of 500 m radius, centred on the centroid of each city park, as the composition of the urban matrix within this radius has already been shown to have severe effects on the species richness and functional diversity of city park bird communities within our study area (Schütz and Schulze 2015). Within circles categories of the land use data describing sealed areas (e.g. roads, buildings etc.) were summarised and their areas were calculated, excluding the park areas. We hypothesise that sealed areas, especially buildings which account for most of them, impede movement of woodpeckers since they indicate a high extent of direct human disturbance and/or do not provide suitable habitat, even for dispersal movements. All spatial analyses were carried out in ArcGIS 10.2 (ESRI).

Statistical analysis

For each woodpecker species we used an information theoretic approach to test for effects of local scale predictor variables (park area, basal area, proportion of tree cover, density of large trees, density of large *Quercus* trees, number of tree genera), regional scale variables (proportion sealed area, distance to nearest breeding site, indices quantifying the connectivity of city parks to other green spaces) and winter in which bird surveys were carried out on the dependent variable park occupancy. Park occupancy was included in the models for each winter separately. In winters in which city parks were surveyed two times, the respective woodpecker species occupied a city park when it could be recorded at least in one of the two surveys. For model selection, we used an all-subset approach, in which all possible combinations of explanatory variables are searched and a subset of models given the most favourable values of the quantitative criterion are identified (Murtaugh 2009; Symonds and Moussalli 2011). Prior to analysis, variables that were not normally distributed were log-transformed (park size, number of tree genera, density of large *Quercus* trees), arc-sin-transformed (proportion of tree cover) or sqrt-transformed (distance to nearest breeding site). To minimise multi-collinearity, we identified correlated local variables using Pearson's Correlation Coefficient. Additionally, as all six connectivity measures quantify the connectivity of city parks to other green spaces and only differ in giving different weight to distance and whether they consider the size of green spaces city parks are connected to or not, all models including more than one network variable were discarded. Each candidate model was therefore comprised of variables that were not strongly correlated ($r < 0.4$) including a maximum of one network variable. We ranked models using Akaike's information criterion corrected for small-sample sizes (AIC_c). Only models that had an AIC_c difference (Δ_i) < 2 were considered in the candidate set (Richards, Whittingham, and Stephens 2011; Symonds and Moussalli 2011) and Akaike weights (= the relative likelihood of the model being the best) of these models were calculated. For all models with an AIC_c difference (Δ_i) < 2 , we used model averaging to compute the average estimates for parameters of interests from all models in a candidate set. Full model averaged estimates were used for graphical representation.

All statistical analyses were carried out in R 3.0.3 (R Core Team 2014), using the R packages ggplot2 (Wickham 2009), glmulti (Calcagno 2013) and MuMIn (Barton 2015). For the whole dataset of local and regional variables used for statistical analyses see Supplementary Tables S1 and S2.

Results

Local and regional scale variables

The mean tree cover of surveyed parks was 40 %, containing a mean number of 50 large trees/ha and one large oak tree/ha. The number of tree genera ranged from 1 to 68, averaging 22 tree genera per park. The basal area within city parks was on average 41 m²/ha and the mean proportion of sealed area surrounding the parks covered 80 %. The distance of a park to the nearest breeding site of Great Spotted Woodpeckers reached from 58 to 1280 m and to those of Middle Spotted Woodpeckers from 207 to 3845m (Supplementary Table S3). The Sigmund Freud Park was the most central one with respect to the number of connected nodes at all three spatial scales. The area weighted connectivity was highest for the Alfred Böhm Park (for location of parks see Fig. 1).

Occurrence of woodpeckers in urban parks

When considering all surveys between 2005 and 2015 the Great Spotted Woodpecker was found in 20 of the 29 city parks considered in the study (69 %), whereas the Middle Spotted Woodpecker occurred only in seven (24 %) parks (Table 1). The occupancy of city parks (GLM: $F_{5,140} = 3.07$, $P = 0.012$) as well as the mean temperature (one-way ANOVA: $F_{5,65529} = 836$, $P < 0.001$) differed between winters. Highest prevalence values were observed in winter 2005/6 which was an extremely cold one (Supplementary Fig. S1). Mean winter temperature and park occupancy were negatively correlated ($\beta = -0.3$, $P < 0.001$).

Model selection

Being included in all of the best ranked models park size represented an important variable in describing the occupancy of city parks by the Great Spotted Woodpecker as well as by the Middle Spotted Woodpecker (Tables 2 and 3). Model averaged estimates indicate a strong positive influence of park size on the occurrence of these two woodpecker species, with much larger area requirements for the Middle compared to the Great Spotted Woodpecker (Fig. 2; Tables 4 and 5). Beside park size no other local scale variable had effects on the city park occupancy by Middle Spotted Woodpeckers. In Great Spotted Woodpeckers tree cover and density of large trees were at least included in the best ranked models. However, model averaged estimates did not show effects of these two variables on the occurrence of the Great Spotted Woodpecker. Basal area, density of large *Quercus* trees and number of tree genera were not included in any of the best ranked models.

Among regional scale variables, the distance to the nearest breeding site as well as some of the connectivity measures were included in the best ranked models of the two woodpecker species. However, they only had a minor effect on describing the occupancy of city parks (Tables 2 – 5). The proportion of sealed area was not included in any of the best ranked models. The winter in which bird surveys were carried out strongly influenced encounter rates of Great Spotted Woodpeckers in city parks (Tables 2 and 4). Highest probabilities of occurrence were gained in the winter 2005/6 (Fig. 3).

Table 2. Seven best ranked models ($\Delta AIC_c < 2$) explaining the occurrence of Great Spotted Woodpecker in Vienna city parks. Akaike's information criterion corrected for small-sample size (AIC_c), differences in AIC_c values of each model compared with the model with the lowest AIC_c value (ΔAIC_c) and the Akaike weights (ω_i) are listed. Grey marked rows indicate variables whose relative importance (sum of Akaike weights over all models in which variable appears) is 1. Black dots indicate variables included in each model.

Predictor variable	1	2	3	4	5	6	7	Relative importance of variable
PA	•	•	•	•	•	•	•	1
BA								
TC		•						0.17
LT							•	0.11
LQ								
TG								
WI	•	•	•	•	•	•	•	1
SA								
DB				•				0.11
CN _{IDW}						•		0.11
CN _{IDW2}					•			0.11
CN _{IDW3}								
CA _{IDW}								
CA _{IDW2}			•					0.13
CA _{IDW3}								
AIC_c	131.78	132.74	133.25	133.62	133.63	133.64	133.71	
ΔAIC_c	0	0.96	1.47	1.84	1.85	1.86	1.93	
ω_i	0.27	0.17	0.13	0.11	0.11	0.11	0.1	

PA, park area; BA, basal area; TC, proportion of tree cover; LT, density of large trees; LQ, density of large *Quercus* trees; TG, number of tree genera; WI, winter in which surveys were carried out; SA, proportion of sealed area; DB, distance to nearest breeding site; CN_{IDW}, connectivity nodes excluding area with linear-weighted distance; CN_{IDW2}, connectivity nodes excl. area with square-weighted distance; CN_{IDW3}, connectivity nodes excl. area with cubic-weighted distance; CA_{IDW}, connectivity nodes including area with linear-weighted distance; CA_{IDW2}, connectivity nodes incl. area with square-weighted distance; CA_{IDW3}, connectivity nodes incl. area with cubic-weighted distance.

Table 3. Five best ranked models ($\Delta AIC_c < 2$) explaining the occurrence of Middle Spotted Woodpecker in Vienna city parks. Akaike's information criterion corrected for small-sample size (AIC_c), differences in AIC_c values of each model compared with the model with the lowest AIC_c value (ΔAIC_c) and the Akaike weights (ω_i) are listed. Grey marked rows indicate variables whose relative importance (sum of Akaike weights over all models in which variable appears) is 1. Black dots indicate variables included in each model. For abbreviations of predictor variables see Table 2.

Predictor variable	1	2	3	4	5	Relative importance of variable
PA	•	•	•	•	•	1
BA						
TC						
LT						
LQ						
TG						
WI						
SA						
DB		•				0.27
CN _{IDW}						
CN _{IDW2}						
CN _{IDW3}						
CA _{IDW}			•			0.13
CA _{IDW2}				•		0.13
CA _{IDW3}					•	0.13
AIC_c	55.19	55.69	57.09	57.11	57.17	
ΔAIC_c	0	0.5	1.9	1.92	1.98	
ω_i	0.34	0.27	0.13	0.13	0.13	

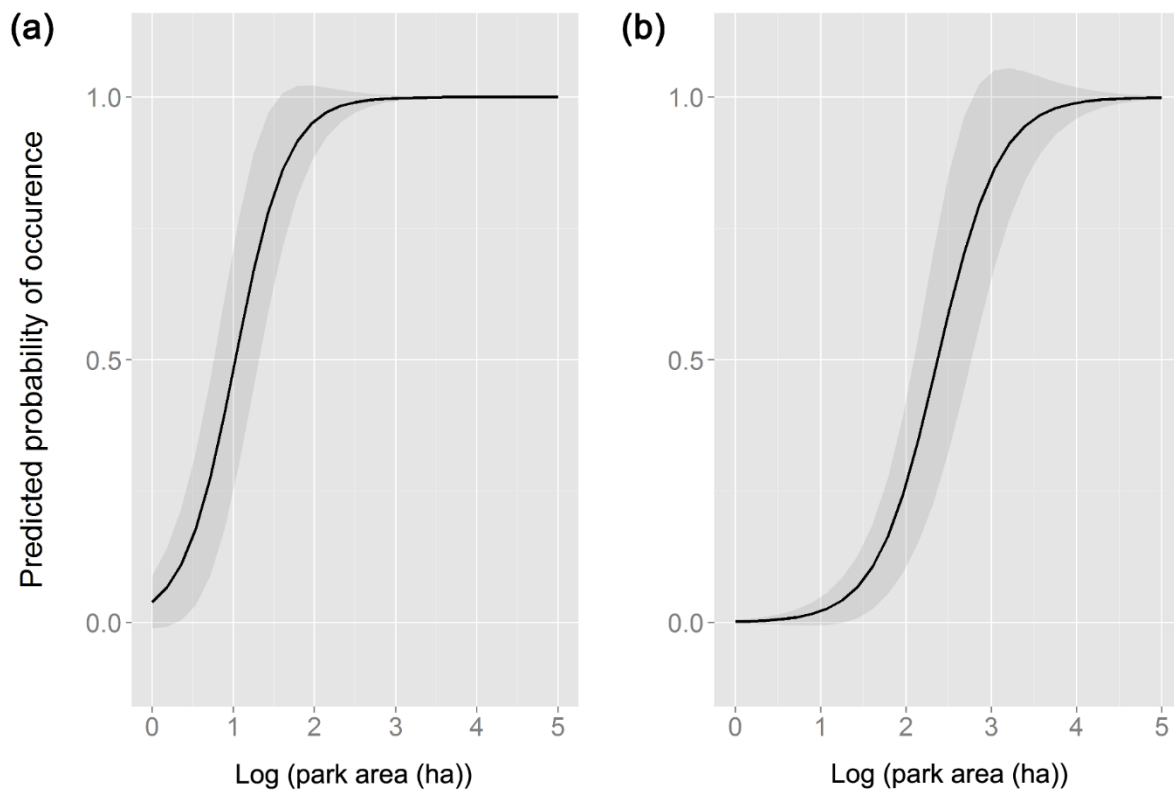


Figure 2. Predicted relationships between park size (ha) and occurrence of the two woodpecker species (a) Great Spotted Woodpecker and (b) Middle Spotted Woodpecker. Predictions are based on model averaged estimates.¹

Table 4. Full model averaged estimates of parameters explaining the occupancy of Vienna city parks by the Great Spotted Woodpecker. Estimates whose confidence intervals do not contain zero are printed in bold. For abbreviations of connectivity measures see Table 2.

Predictor variable	Estimate	SE	Adjusted SE	95 % CI
Intercept				
Winter 2005/2006	-2.03	0.98	0.99	-3.98 – -0.09
Winter 2008/2009	-1.63	0.96	0.97	-3.54 – 0.27
Winter 2009/2010	-3.27	1.01	1.02	-5.27 – -1.26
Winter 2012/2013	-1.32	0.84	0.85	-2.99 – 0.34
Winter 2013/2014	-1.55	0.85	0.86	-3.23 – 0.14
Winter 2014/2015	-2.96	0.96	0.97	-4.85 – -1.06
Park area	3.13	0.57	0.57	2.02 – 4.26
Prop. of tree cover	0.42	1.29	1.3	-2.12 – 2.95
CA _{IDW2}	-0.03	0.12	0.12	-0.26 – 0.20
Distance nearest breeding site	-0.02	0.01	0.01	-0.04 – 0.02
CN _{IDW2}	-0.02	0.09	0.09	-0.19 – 0.16
CN _{IDW}	-0.01	0.09	0.09	-0.18 – 0.15
Density of large trees	0.01	0.05	0.05	-0.01 – 0.01

¹ Slightly modified; a request for a correction note was sent to the Journal of Urban Ecology in July 2018

Table 5. Full model averaged estimates of parameters explaining the occupancy of Vienna city parks by the Middle Spotted Woodpecker. Estimates whose confidence intervals do not contain zero are printed in bold. For abbreviations of connectivity measures see Table 2.

Predictor variable	Estimate	SE	Adjusted SE	95 % CI
Intercept	-6.1	1.8	1.81	-9.63 – -2.55
Park area	2.79	0.59	0.59	1.63 – 3.96
Distance nearest breeding site	-0.01	0.03	0.03	-0.11 – 0.03
CA _{IDW}	-0.02	0.15	0.15	-0.91 – 0.58
CA _{IDW2}	-0.03	0.24	0.24	-1.47 – 0.98

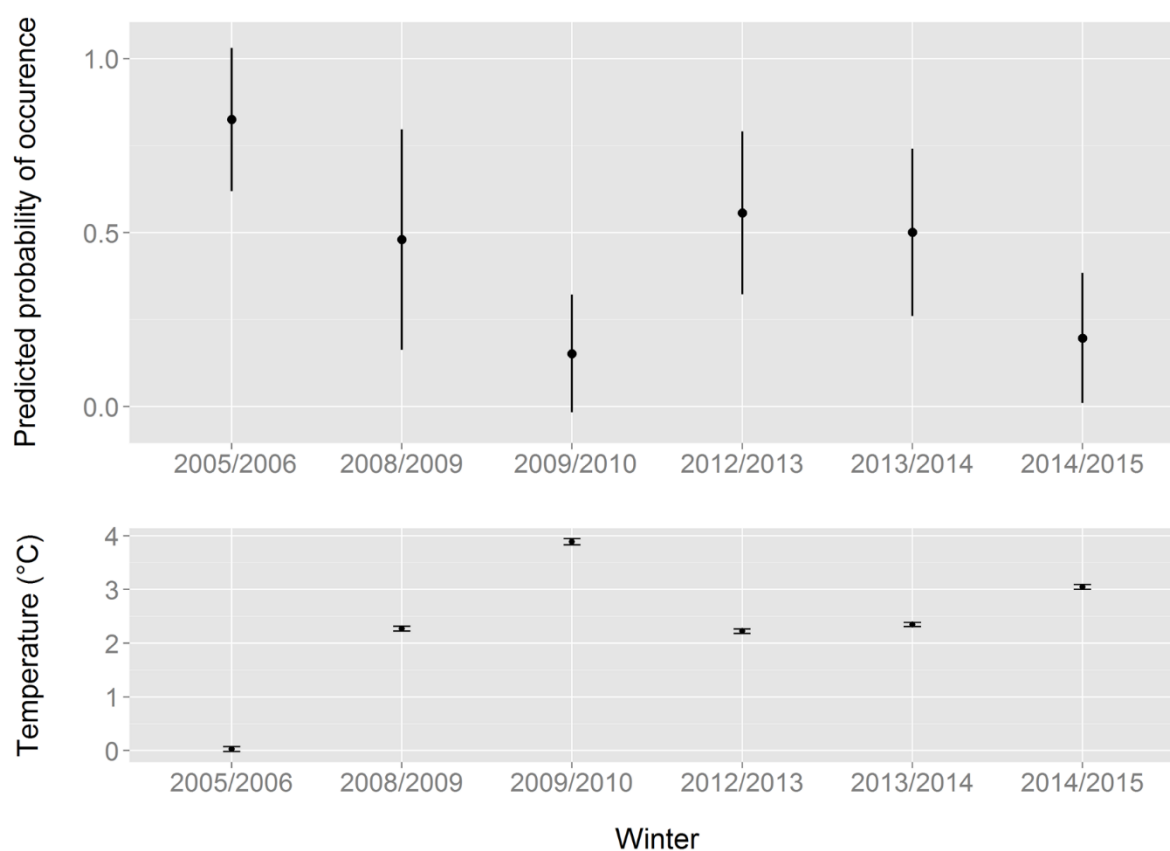


Figure 3. Predicted relationships between winter in which bird surveys were carried out and occurrence of the Great Spotted Woodpecker. Predictions are based on model averaged estimates. For a better comparison between severity of winter and probability of woodpecker occurrence also mean winter temperatures (\pm SE) are indicated.

Discussion

Among local habitat variables park size was the only significant predictor for the occurrence of woodpecker species in our study. In accordance with other studies patch size had a positive effect on the occurrence of Middle Spotted Woodpecker and Great Spotted Woodpecker (Kosiński 2006; Myczko et al. 2014). Large city parks – as remnants of semi-natural green space embedded in an urban landscape – have larger core areas that are unaffected by edge effects associated with the surrounding matrix, such as higher levels of car and pedestrian traffic (Fernández-Juricic 2001). Woodpeckers may then find suitable habitats in the more undisturbed core areas of large city parks. Moreover, a study on patch-occupancy dynamics of Middle Spotted Woodpeckers demonstrated a higher persistence in larger forest fragments (Robles and Ciudad 2012). Further, local extinctions can be buffered by floaters. Such non-breeding birds capable of replacing lost territorial individuals were more abundant in larger high-quality patches (Robles and Ciudad 2017). As woodpeckers are territorial species and can occupy home ranges almost year-round, these described metapopulation dynamics may also be applied to woodpeckers inhabiting green space remnants embedded in an urban matrix (Myczko et al. 2014). Hence, the higher occurrence probability of woodpeckers in large city parks may be the result of a higher persistence caused by a lower extinction risk within these patches.

Great Spotted Woodpeckers, representing by far the most abundant woodpecker species of Vienna, showed higher probabilities of occurrence in smaller parks compared to the Middle Spotted Woodpecker, classified as forest insectivorous specialist and having situated its population stronghold in mature woodlands on the outskirts of Vienna (Mikusiński and Angelstam 1997; Wichmann et al. 2009). This is in accordance with a study carried out in Poland showing that the mean size of forest plots occupied by Middle Spotted Woodpeckers were larger than that of Great Spotted Woodpeckers, underlining the area-demanding character of this species (Kosiński 2006).

Beside park size other local scale variables were of minor importance in explaining the occurrence of the two woodpecker species. For the Middle Spotted Woodpecker the density of large oaks has often been stressed to be a key requisite in its habitat (Pasinelli 2003; Robles and Ciudad 2012; Robles and Ciudad 2017). This was not supported by the results of our study, with density of large oaks not even being included in the best ranked models. However, Middle Spotted Woodpeckers are not only associated with mature stands of oaks, but with large deciduous trees in general (Kosiński 2006, Roberge, Angelstam, and Villard 2008). As city parks considered in this study are dominated by deciduous tree species, covering on average $85 (\pm 16) \%$ of large trees (> 30 cm) – a variable included in our analyses – we did not incorporate the density of large deciduous trees as additional separate variable. Despite being considered as a more generalist species also Great Spotted Woodpeckers show a marked habitat selection, preferring well forested habitat patches with a high diversity of tree species and a high density of large trees (Barrientos 2010; Segura 2017). Although the proportion of tree cover as well as the density of large trees were included in the best ranked models of this species, model-averaged estimates did not show a strong effect of these variables on the species' occurrence in our study. That no effect (Middle Spotted Woodpecker) or only a weak one (Great Spotted Woodpecker) of large trees on the occurrence of woodpeckers could be detected may be related to (1) the small variation in large tree density between studied city parks and/or (2) to their generally high density. Hence large trees may not represent a limiting structure for foraging woodpeckers.

Studies on habitat preferences of woodpeckers predominantly focused on the breeding season, but differences in habitat selection between breeding season and winter months could already be observed. Between October and December Middle Spotted Woodpeckers for example showed an expansion into less mature forest areas (lower forest cover and fewer large trees) with a greater abundance of dead trees (Domínguez, Carbonell, and Ramírez 2017). The density of dead trees also promotes the

occurrence of the Great Spotted Woodpecker (Segura 2017). However, almost every park considered in this study is open to public. Consequently, due to potential safety and aesthetic reasons the removal of standing dead wood is forced by city authorities (Sandström, Angelstam, and Mikusiński 2006; Aronson 2017). Because of these park management measures dead wood within city parks may be a limited resource being of minor importance in determining the occurrence of the two woodpecker species.

At a regional scale neither network connectivity assessed at three spatial scales, nor patch isolation, quantified as the distance to the nearest breeding site, had an effect on the presence of woodpeckers. Also the proportion of sealed area surrounding each city park did not influence the occupancy of city parks by the two woodpecker species. Hence, the permeability of the urban matrix appears being neglectable for explaining the winter distribution of both woodpecker species in city parks in our study area. This is in accordance with theoretical predictions that specialist species with specific habitat needs are predominately governed by local variables as they tend to monopolise restricted resources in fragmented habitats (Pandit, Kolasa, and Cottenie 2009; Dapporto and Dennis 2013; Funk, Schiemer, and Reckendorfer 2013). Hence, local scale park variables rather than regional scale landscape variables may be linked to the probability of park occupancy. In contrast, generalists benefit from using any suitable resources (Dapporto and Dennis 2013). Consequently, regional scale variables may be of major importance when occupying city parks. Based on these theoretical assumptions, we expected some association with variables operating on a regional scale, such as landscape permeability and connectivity, at least for the Great Spotted Woodpecker, the most widely distributed and one of the least specialised woodpecker species (Mikusiński and Angelstam 1997). However, also other studies provided only weak evidence, that woodpeckers may be governed by regional variables. In Örebro in Sweden the number of woodpecker species as well as the number of individuals increased from the city centre to the periphery, supposing some influence of regional landscape configuration on species distribution (Sandström, Angelstam, and Mikusiński 2006).

Similar results were reported by Myczko et al. (2014) who found a comparable trend with woodpeckers to be less common and abundant in the city centre. But in both studies the spatial configuration of the landscape only explained a small proportion of variability in the data. Furthermore, regional and habitat variables could not be properly disentangled. For example, in Myczko et al. (2014) the regional urbanisation index was correlated with deciduous forest and patch area.

A meta-analysis of factors determining intra-urban biodiversity of different taxonomic groups (including birds) also found only weak support for the significance of connectivity variables, but a strong effect of functional corridors (Beninde et al. 2015). A positive effect of corridors on birds of the urban landscape has regularly been reported (Fernández-Juricic and Jokimäki 2001). Shanahan et al. (2011) for instance reported significant effects of revegetated areas directly connected with remnant vegetation (i.e. a maximum gap width < 50 m to the analysed patch) on bird diversity and abundance. The small gap width was presumably chosen because many forest birds are reluctant to leave the forest, and even small gaps seem to hinder movement on a short-term basis (Bélisle and Desrochers 2002). On a larger temporal scale such gaps may be irrelevant for dispersal, i.e. there is no apparent dispersal limitation (Whittaker and Marzluff 2012). Dispersal limitation is a function of scale (temporal and spatial) and the species under consideration. When considering breeding dispersal for instance, inter-patch distances < 3.5 km have no significant influence on the distribution of the nuthatch (*Sitta europea*). Only if inter-patch distances increased above 3.5 km dispersal limitation were evident (Van Langevelde 2000). The Nuthatch has similar breeding dispersal abilities such as the investigated woodpeckers with median values of 1.67 km (Matthysen, Adriaensen, and Dhondt 1995). For juvenile Middle Spotted Woodpeckers dispersal distances range from 0.9 to 4.8 km in fragmented landscapes (Ciudad,

Robles, and Matthysen 2009) and in Great Spotted Woodpeckers the median natal dispersal is estimated 6 km (Gil-Tena et al. 2013). Furthermore, woodpeckers are not strictly sedentary species, but rather show nomadic migration movements. The intensity of these movement patterns is predominantly triggered by food shortage and high population densities (Newton 2006; Linden et al. 2011). Adverse circumstances can cause individuals to disperse even hundreds of kilometres (Newton 2006). Given these high dispersal abilities of birds and the low explanatory power of direct connectivity measures, it seems unlikely that dispersal limitation plays a significant role in structuring bird communities in cities with a high amount of green space such as Vienna. For the investigated parks, the minimum distance to the next green space remnant averages 334 m (minimum: 119 m, maximum: 546 m), which is significantly less than the reported dispersal potential of the two woodpecker species.

The reported positive effects of corridors and surrounding green space are presumably a surrogate for the enlargement of the patch area itself. The effects of corridors in promoting biodiversity may be based on an enlargement of patch area or on an increase of connectivity between patches, i.e. the effects of area and corridors are difficult to disentangle, what was also pointed out by Shanahan et al. (2011).

Beside corridors, also percentage of surrounding green space was revealed as important parameter in determining urban biodiversity (Beninde et al. 2015). Depending on the dispersal ability of different species, again surrounding green space can act as a landscape variable related to connectivity or simply as an extension of the patch area under consideration.

Our results point out the importance of city parks as refuges for birds during cold winters. For Great Spotted Woodpeckers the winter in which bird surveys were carried out was an important variable in explaining the encounter rates of this species in city parks. Highest probabilities of occurrence were recorded in the winter 2005/6, which also was the coldest one among survey years. During winter time birds face high thermoregulatory costs emerging especially from long, cold nights (Pinowski et al. 2006). As the time window available for foraging is shortened at this time of the year and resources are depleted, compensating these metabolic losses is challenging. By dispersing from rural to urban areas woodpeckers may find sufficient food supply even under adverse circumstances (Tryjanowski et al. 2015). Indeed, decreasing temperatures lead to higher encounter rates of Great Spotted Woodpeckers at artificial bird feeders (Chamberlain et al. 2005). Additionally, higher artificial light levels in urban areas may enable birds to prolong their diurnal foraging activity (Russ, Rüger, and Klenke 2015). Furthermore, due to the urban heat island phenomenon built up areas of the city centre of Vienna show higher air temperatures than the surrounding rural areas, being most noticeable during summer and winter (Böhm 1998). Hence, thermoregulatory stress during cold winter nights may be reduced by inhabiting urban areas. A more intense use of urban areas during winter time may increase the probability of park occupancy by Great Spotted Woodpeckers. There was no effect of survey winter on the park occupancy by Middle Spotted Woodpeckers maybe due to low sample size.

In conclusion, it seems that the size of habitat patches rather than their position within the landscape matrix is important for birds in general and woodpeckers in particular. We thus recommend park areas > 20 ha to promote woodpecker habitats. Parks of this size are likely to be occupied by Great Spotted Woodpeckers and the occurrence probability of Middle Spotted Woodpeckers would exceed 75 %. The proposed size is above the range of threshold values reported to promote generalist bird species in cities (1-10 ha), but is still at the lower end of values recommended to promote area-sensitive species (20-140 ha) (Beninde et al. 2015).² Nevertheless, this size will allow the occurrence of the two woodpecker species and thereby foster facultative and obligatory cavity-using species such as passerines,

² Slightly modified; a request for a correction note was sent to the Journal of Urban Ecology in July 2018

mammals and insects as at least the Great Spotted Woodpecker – being widely distributed across the city of Vienna and even inhabiting heavily built-up areas (Wichmann et al. 2009) – might use some of the city parks also for breeding and thereby ensures nest availability. As in big cities an enlargement of city parks is difficult to realise, the implementation and maintenance of corridors such as alley trees along roads or scattered greenery of public space – especially among city parks of high quality – may be a cost efficient alternative (Fernández-Juricic and Jokimäki 2001). At least corridors being wisely designed and managed may then disproportionally enlarge the patch area of remnant green spaces, as the size of the new patch area equals the sum of two patches plus corridor area. This may also be a first approach to promote area sensitive species in cities.

The fact that large trees are still a prominent feature in most city parks of Vienna and that their density is fairly similar between parks, may additionally promote the importance of park size in explaining the occurrence of the two woodpecker species because in larger parks they have better chances to meet their foraging and shelter requirements. But this also means that a loss of large trees – even if the size of the habitat patch remains stable – can cause severe declines in woodpecker populations inhabiting fragmented landscapes (Pasinelli 2000).

Hence, beside the implementation and maintenance of ‘green’ corridors to enlarge the size of remnant habitat patches, care must be also taken to preserve large trees within city parks in order to promote woodpecker occurrence in urban landscapes.

Data availability

All woodpecker data used in this study are available as Supplementary data.

Supplementary data

Supplementary data are available at JUECOL online.

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Conflict of interest statement

None declared.

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Supplementary Information

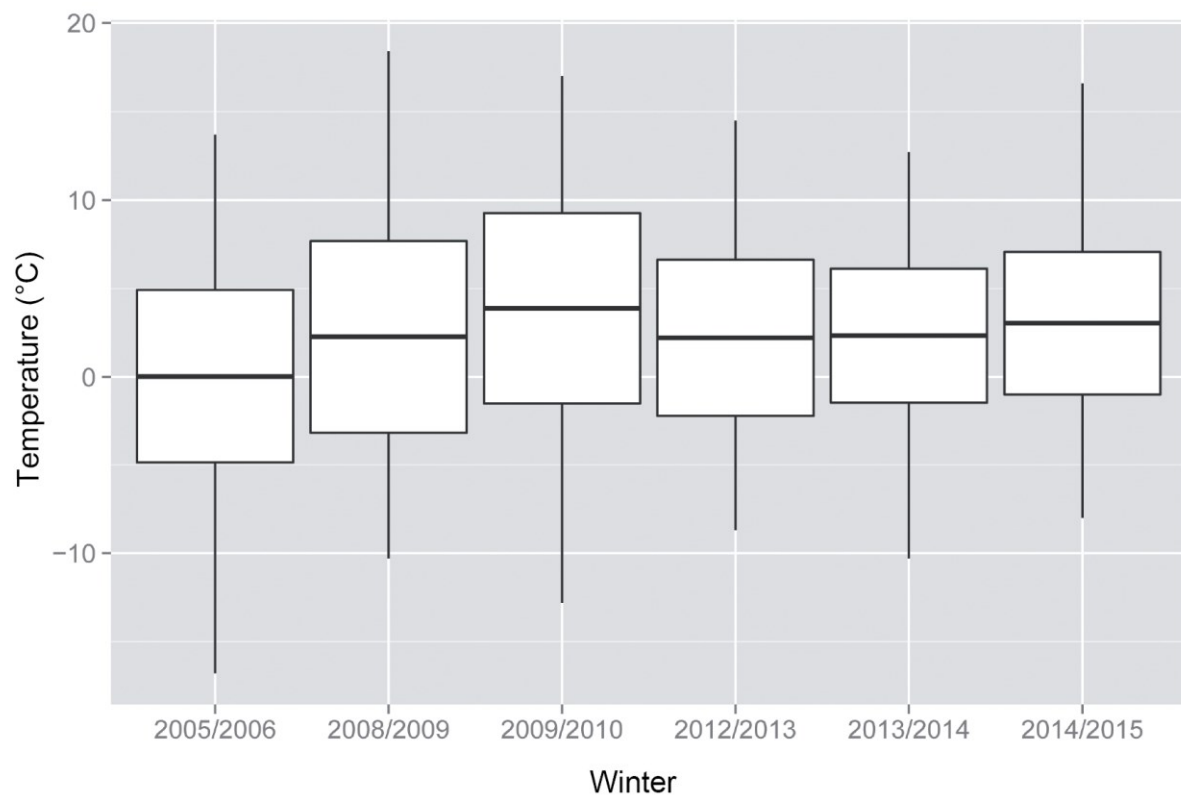


Figure S1. Mean temperature of winters in which bird surveys were carried out. Boxes indicate standard deviation, whiskers minimum and maximum values. Each winter includes temperatures of November, December and January based on a daily 10 min interval (<https://meteo.boku.ac.at/wetter/mon-archiv>).

Table S1. Local scale variables of 29 Vienna city parks considered for analyses. To improve the fit to normality the variables park size, density of large oaks and number of tree genera were log-transformed ($\log x + 1$), while the proportion of canopy cover was arc-sin transformed.

City park	Log (park area (ha) + 1)	Basal area (m ² /ha)	Arcsin (prop. canopy cover)	Density large trees (no./ha)	Log (density large <i>Quercus</i> (no./ha) + 1)	Log (no. of tree genera + 1)
Albert-Dub-Park	0.64	23.981	0.31	49.44	0	2.4
Alfred Böhm Park	1.33	50.962	0.55	89.49	1.45	3.18
Alfred-Grünwald-Park	0.59	5.882	0.26	33.33	0	2.71
Arenbergpark	1.35	41.444	0.46	47.55	0.87	3.53
Börsepark	0.31	10.453	0.43	66.67	0	1.95
Bruno-Kreisky-Park	0.84	14.924	0.33	44.70	0	2.71
Clemens-Hofbauer-Platz	0.46	8.019	0.41	57.63	0	2.2
Clemens-Krauss-Park	0.47	2.2	0.3	23.33	0	0.69
Esterhazypark	0.68	13.172	0.24	45.36	0	2.83
Fridtjof-Nansen-Park	2.02	42.463	0.27	35.88	0	3.18
Grete Rehor Park	0.52	12.804	0.42	66.18	1.37	2.94
Hügelpark	0.76	26.168	0.37	70.43	1.28	2.89
Kongresspark	1.72	103.22	0.41	68.85	1.22	3.83
Martin-Luther-King	1.09	18.111	0.47	43.94	0.92	2.94
Märzpark	0.95	18.934	0.27	47.47	0	3.14
Ölzelpark	0.74	19.208	0.58	61.82	0	3.04
Rathauspark	1.7	86.629	0.49	54.14	1.03	3.81
Reinlpark	0.44	4.785	0.1	40	0	2.3
Rohrauerpark	0.71	12.717	0.29	47.12	0	2.89
Rudolfspark	0.54	7.466	0.38	45.07	0	2.94
Schillerpark	0.62	8.312	0.48	41.18	0	2.89
Schönbornpark	0.72	13.784	0.38	40.95	0.67	3.22
Schubertpark	0.84	19.476	0.3	44.70	0.56	3.3
Sigmund-Freud-Park	0.91	12.948	0.2	42.86	0	3.14
Stadtpark	2.67	150.424	0.31	41.60	0.60	3.97
Steinbauerpark	0.76	8.788	0.31	24.78	0	2.3
Türkenschanzpark	2.8	371.569	0.5	82.99	1.03	4.23
Waldmüllerpark	1.68	68.288	0.47	66.44	0.38	3.58
Wilhelmsdorfer Park	1.16	8.435	0.26	12.27	0	2.48

Table S2. Regional scale variables of 29 Vienna city parks considered for analyses. To improve the fit to normality the distance to nearest breeding site for Great Spotted Woodpecker (GSW) and Middle Spotted Woodpecker (MSW) were sqrt-transformed. All connectivity measures were standardised ((raw value - mean)/standard deviation). CN_{IDW} – connectivity nodes excluding area with linear-weighted distance, CN_{IDW2} – connectivity nodes excl. area with square-weighted distance, CN_{IDW3} – connectivity nodes excl. area with cubic-weighted distance, CA_{IDW} – connectivity nodes including area with linear-weighted distance, CA_{IDW2} – connectivity nodes incl. area with square-weighted distance, CA_{IDW3} – connectivity nodes incl. area with cubic-weighted distance.

City park	Prop. sealed area	Dist. nearest breeding site GSW (m)	Dist. nearest breeding site MSW (m)	CN _{IDW} _stan	CN _{IDW2} _stan
Albert-Dub-Park	0.61	17.09	29.70	-1.033	-0.92
Alfred Böhm Park	0.69	32.37	62.01	0.728	0.573
Alfred-Grünwald-Park	0.92	14.21	60.88	0.595	-0.26
Arenbergpark	0.84	17.46	38.62	-0.116	-0.538
Börsepark	0.93	21.54	57.43	0.472	0.242
Bruno-Kreisky-Park	0.85	16.63	44.79	1.235	1.519
Clemens-Hofbauer-Platz	0.87	28.30	46.53	-0.721	-0.846
Clemens-Krauss-Park	0.66	31.11	40.91	-0.685	-0.253
Esterhazypark	0.91	23.16	55.71	0.666	-0.082
Fridtjof-Nansen-Park	0.52	20.29	46.86	-1.532	-0.314
Grete Rehor Park	0.83	15.31	59.88	1.117	1.665
Hügelpark	0.51	9.73	33.92	-1.94	-1.386
Kongresspark	0.43	19.11	40.97	-1.089	-0.195
Martin-Luther-King	0.74	34.40	50.40	0.704	-0.207
Märzpark	0.83	35.77	50.29	0.219	0.031
Özeltpark	0.89	18.83	33.46	-2.56	-1.124
Rathauspark	0.87	18.25	57.21	0.846	0.603
Reinlpark	0.81	7.61	34.32	-0.677	-0.732
Rohrauerpark	0.73	19.57	48.29	-0.961	-1.166
Rudolfspark	0.88	28.12	56.70	0.193	-0.018
Schillerpark	0.86	17.58	58.35	0.863	1.378
Schönbornpark	0.87	14.24	52.80	0.536	0.073
Schubertpark	0.79	17.30	32.30	-0.374	-0.429
Sigmund-Freud-Park	0.89	12.63	54.19	1.467	4.238
Stadtpark	0.92	17.11	48.12	-0.156	-0.801
Steinbauerpark	0.82	24.18	38.92	0.919	0.255
Türkenschanzpark	0.5	14.38	14.38	-0.724	-0.609
Waldmüllerpark	0.87	24.93	58.58	0.657	-0.297
Wilhelmsdorfer Park	0.82	30.03	38.27	0.734	-0.032

Table S2 (continued). Regional scale variables of 29 Vienna city parks considered for analyses. To improve the fit to normality the distance to nearest breeding site for Great Spotted Woodpecker (GSW) and Middle Spotted Woodpecker (MSW) were sqrt-transformed. All connectivity measures were standardised ((raw value – mean)/standard deviation). CN_{IDW} – connectivity nodes excluding area with linear-weighted distance, CN_{IDW2} – connectivity nodes excl. area with square-weighted distance, CN_{IDW3} – connectivity nodes excl. area with cubic-weighted distance, CA_{IDW} – connectivity nodes including area with linear-weighted distance, CA_{IDW2} – connectivity nodes incl. area with square-weighted distance, CA_{IDW3} – connectivity nodes incl. area with cubic-weighted distance.

City park	CN _{IDW3} _stan	CA _{IDW} _stan	CA _{IDW2} _stan	CA _{IDW3} _stan
Albert-Dub-Park	-0.595	2,883.886	1,201.838	1,155.213
Alfred Böhm Park	0.05	4,326.142	2,072.293	1,869.074
Alfred-Grünwald-Park	-0.42	3,775.579	1,472.602	1,064.924
Arenbergpark	-0.439	3,680.864	1,492.578	1,126.092
Börsepark	-0.099	3,545.231	1,471.596	1,283.707
Bruno-Kreisky-Park	1.291	4,199.3	4,383.355	21,634.798
Clemens-Hofbauer-Platz	-0.564	2,887.75	798.393	432.209
Clemens-Krauss-Park	0.019	2,889.858	1,191.984	2,424.654
Esterhazypark	-0.304	3,615.413	1,170.133	636.351
Fridtjof-Nansen-Park	-0.244	2,737.993	960.7	854.995
Grete Rehor Park	1.15	3,931.343	2,989.712	7,203.399
Hügelpark	-0.636	3,346.885	1,411.334	1,263.384
Kongresspark	0.203	2,613.781	663.528	485.188
Martin-Luther-King	-0.431	4,068.718	1,514.035	920.958
Märzpark	09	3,407.604	1,265.634	1,698.415
Özeltpark	-0.478	2,501.176	833.361	922.746
Rathauspark	0.041	3,640.949	1,870.031	2,595.011
Reinlpark	-0.487	3,491.341	1,282.335	820.406
Rohrauerpark	-0.664	3,014.821	771.181	290.26
Rudolfspark	-0.144	3,501.052	1,346.444	1,025.554
Schillerpark	1.600	3,927.97	2,252.719	3,972.919
Schönbornpark	-0.264	3,435.703	1,361.138	1,259.331
Schubertpark	-0.318	3,076.168	1,122.602	948.434
Sigmund-Freud-Park	5.187	3,596.963	2,044.759	5,133.202
Stadtpark	-0.562	3,540.054	1,305.529	846.347
Steinbauerpark	-0.214	4,088.568	1,763.094	1,615.147
Türkenschanzpark	-0.44	2,882.982	1,418.827	2,164.566
Waldmüllerpark	-0.443	3,897.437	1,339.597	767.885
Wilhelmsdorfer Park	-0.341	4,106.276	1,666.132	1,234.614

Table S3. Detailed overview of local and regional scale variables of 29 Vienna city parks considered for analyses. For abbreviations of connectivity measures see Table S2.

Variable	Unit	Mean \pm SD	Min	Max
<i>Local scale variables</i>				
Park area	ha	2.7 \pm 3.6	0.4	15.5
Basal area	m ² /ha	41 \pm 72	2.2	371.6
Proportion tree cover	-	0.4 \pm 0.1	0.1	0.6
Density of large trees (DBH > 30 cm)	no. of trees/ha	50 \pm 17	12	89
Density of large <i>Quercus</i> trees (DBH \geq 37 cm)	no. of trees/ha	1 \pm 1	0	3
Number of tree genera	-	22 \pm 15	1	68
<i>Regional scale variables</i>				
Proportion sealed area	-	0.8 \pm 0.1	0.43	0.9
Distance to the nearest breeding site				
- Great Spotted Woodpecker	m	481 \pm 332	58	1280
- Middle Spotted Woodpecker	m	2278 \pm 991	207	3845
CN _{IDW}	-	0 \pm 1	-2.56	1.47
CN _{IDW2}	-	0 \pm 1	-1.39	4.24
CN _{IDW3}	-	0 \pm 1	-0.66	5.19
CA _{IDW}	-	0 \pm 1	-1.93	1.65
CA _{IDW2}	-	0 \pm 1	-1.26	4.19
CA _{IDW3}	-	0 \pm 1	-0.53	5.51

2.3. Park size and prey density limit occurrence of Eurasian Sparrowhawks in urban parks during winter

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Schütz C. & C. H. Schulze: Park size and prey density limit occurrence of Eurasian Sparrowhawks in urban parks during winter.

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Abstract

Background: Eurasian Sparrowhawks (*Accipiter nisus*) increasingly represent successful city-dwellers. Thereby, a rich food supply indicated by high numbers of small birds is believed to be the key driver for this bird-eating raptor species to settle in urban environments. However, as small passerine birds show particularly strong antipredator responses, Sparrowhawks may not simply focus on patches of highest prey densities, but rather respond strategically to prey behavior, raising the importance of other parameters in determining the occurrence within urban landscapes.

Methods: To deepen our knowledge on habitat requirements of urban Sparrowhawks, bird surveys were carried out during winter between December 2005 and January 2017 in 36 city parks in Vienna, Austria. Beside food supply also park size, canopy heterogeneity and the connectivity with other green spaces were considered.

Results: Occurrence of Sparrowhawks was positively affected by increasing park size, prey density and the interaction between both. Bird feeder density and park connectivity with other green spaces were of minor importance in explaining the presence of this species. Canopy heterogeneity didn't affect city park occupancy by Eurasian Sparrowhawks.

Conclusions: Our results suggest that large city parks, particularly when characterized by high prey densities, substantially contribute to protect and preserve ecologically important bird species such as raptors within the urban environment – a landscape already struggling with biodiversity losses and functional homogenization.

Keywords

Birds of prey, bird feeders, prey abundance, habitat connectivity, tree cover, urban ecology

Own contribution

Study design: 50 %, data collection: 25 %, statistical analyses: 90 %, manuscript preparation: 100 %

Background

While many raptor species are susceptible to human disturbance and habitat modification, hence avoiding urbanized areas, others have successfully colonized towns and cities during the last decades and are now increasingly associated with such strongly human-dominated areas (Kettel et al. 2018). Raptor species capable of utilizing urban habitats often benefit from their ample prey availability (Chace and Walsh 2006; Gahbauer et al. 2015; Lin et al. 2015; Suri et al. 2017; but compare Sumasgutner et al. 2014). In particular increased abundances of small mammalian human-commensals and passerines, both being attracted by artificial feeding opportunities, promote the occurrence of several falcon and *Accipiter* species in urban environments (Chace and Walsh 2006; Rutz 2008). Additionally, road traffic noise masks avian alarm calls, impeding the ability of passerine birds to perceive these critical signals (Templeton et al. 2016). As a consequence, hunting attempts of raptors may be more successful in noise-polluted urban environments. Further, birds of prey colonizing highly urbanized areas may benefit from reduced numbers of natural predators (Tella et al. 1996; Lin et al. 2015) and the buffering of urban environments against harsh weather conditions (“heat island effect”: Gartland 2011; Lin et al. 2015).

Also the Eurasian Sparrowhawk (*Accipiter nisus*) is increasingly associated with towns, or even large cities and tends to become a successful city-dwelling bird (Newton 2010; Papp 2011). Sparrowhawks breeding in urban habitats can even have a higher reproductive success than those nesting in rural areas (Thornton et al. 2017). Sufficient food supply indicated by high numbers of small birds is believed to be the key resource when settling in urban habitats (Newton 2010). Hence, city parks with a rich food supply may be frequently occupied by Sparrowhawks. This may be particularly important during winter, when large numbers of small passerines are attracted to bird feeders (Jokimäki and Suhonen 1998). However, prey species of Sparrowhawks usually have particularly strong antipredator responses such as alarm or mobbing calls (Hogstad 1995; Forsman and Mönkkönen 2001). Hence, a warning call from just one individual is enough to make all the small birds flush to safe cover (Newton 2010). Additionally, the ‘many-eyes’ effect of high density prey flocks increases the probability of a predator being detected and allowing the prey to escape in time (Pulliam 1973). As Sparrowhawks are ambush hunters and rely on the moment of surprise during hunting, these efficient defense mechanisms of their prey may force the predator to adopt alternative hunting strategies than just focusing on prey density hotspots (Roth II and Lima 2007). Indeed, studies on bird-eating Sharp-Shinned Hawks (*Accipiter striatus*) have already shown that hawks maintain spatial and temporal unpredictability in their movements instead of focusing on areas with high prey densities. Further, their hunting attempts proved more successful when attacking solitary feeding prey than prey foraging in groups (Roth II et al. 2006; Roth II and Lima 2007).

In this study we investigated if the occurrence of Eurasian Sparrowhawks in city parks simply follows classical concepts of foraging theory, with predators choosing patches of highest prey densities, or if this small raptor rather responds strategically to prey behavior, raising the importance of other parameters in predicting its occurrence within urban parks (Lima 2002). Hence, beside food supply also park size and the degree of canopy cover heterogeneity within city parks should be considered. The proportion of undisturbed core areas increases with park size (Fernández-Juricic 2001), facilitating the species to find suitable spots for plucking, roosting and resting – the main demands on its rural wintering habitats (Ortlieb 1995). As Sparrowhawks are known to hunt extensively along forest edges (Götmark and Post 1996), a high degree of canopy heterogeneity may contribute substantially to the suitability of city parks as hunting grounds.

Also the habitat surrounding city parks may affect the occurrence of Eurasian Sparrowhawks as a high number of green spaces in close vicinity to the city parks provide additional hunting grounds. In

contrast, in highly sealed urban areas the available habitat for passerine prey species may predominantly be confined to the urban park (Moudrá et al. 2018), possibly making it less attractive to the Sparrowhawk, independent of its own suitability for this small raptor.

Methods

Study area

The study was conducted in Vienna (48°13' N, 16°22' E), the capital of Austria, being inhabited by 1.9 million people and covering an area of 415 km² (Statistics Austria 2017). We chose 36 urban parks with a mean area of 6.2 ha ranging from 0.36 to 34.48 ha, and spread across the city centre of Vienna (Fig. 1, Table 1).

Table 1. Habitat characteristics of city parks considered in this study. City park codes refer to numbers in Fig. 1.

City park code	Park name	Area (ha)	Canopy heterogeneity	CA _{IDW}
1	Alfred-Böhm-Park	2.76	0.07	4,371
2	Alfred-Grünwald-Park	0.81	0.22	3,801
3	Allerheiligenpark	2.14	0.09	2,971
4	Alois-Drasche-Park	1.98	0.12	4,014
5	Arenbergpark	2.86	0.11	3,772
6	Auer-Welsbach-Park	14.20	0.16	4,296
7	Augarten	34.48	0.11	3,093
8	Börsepark	0.36	0.09	3,611
9	Botanischer Garten	9.63	0.09	4,444
10	Burggarten	2.91	0.17	3,864
11	Casinopark Baumgarten	4.32	0.14	2,763
12	Esterhazypark	0.97	0.19	3,650
13	Fridtjof-Nansen-Park	6.55	0.15	2,756
14	Friedhof St. Marx	6.72	0.02	3,784
15	Grete-Rehor-Park	0.68	0.18	3,974
16	Haydnpark	2.05	0.07	4,056
17	Heiligenstädter Park	7.96	0.08	2,649
18	Hugo-Wolf-Park	5.86	0.07	2,959
19	Kongresspark	4.59	0.14	2,651
20	Liechtensteinpark	4.82	0.10	3,370
21	Napoleonwald	3.14	0.10	2,604
22	Ölzelpark	1.10	0.07	2,519
23	Ostarrichipark	1.05	0.13	3,680
24	Park der Universitätssternwarte	5.82	0.01	3,249
25	Penzinger Friedhof	4.54	0.10	3,292
26	Rathauspark	4.47	0.09	3,692
27	Schweizergarten	15.91	0.10	4,082
28	Stadtpark	13.39	0.13	3,563
29	Steinbauerpark	1.13	0.09	4,137
30	Türkenschanzpark	15.52	0.11	2,945
31	Vogelweidpark	1.81	0.15	3,366
32	Volkspark	19.19	0.10	4,342
33	Währingerpark	6.79	0.12	3,042
34	Waldmüllerpark	4.38	0.07	3,961
35	Wertheimsteinpark	6.78	0.10	2,891
36	Wilhelmsdorferpark	2.20	0.14	4,153

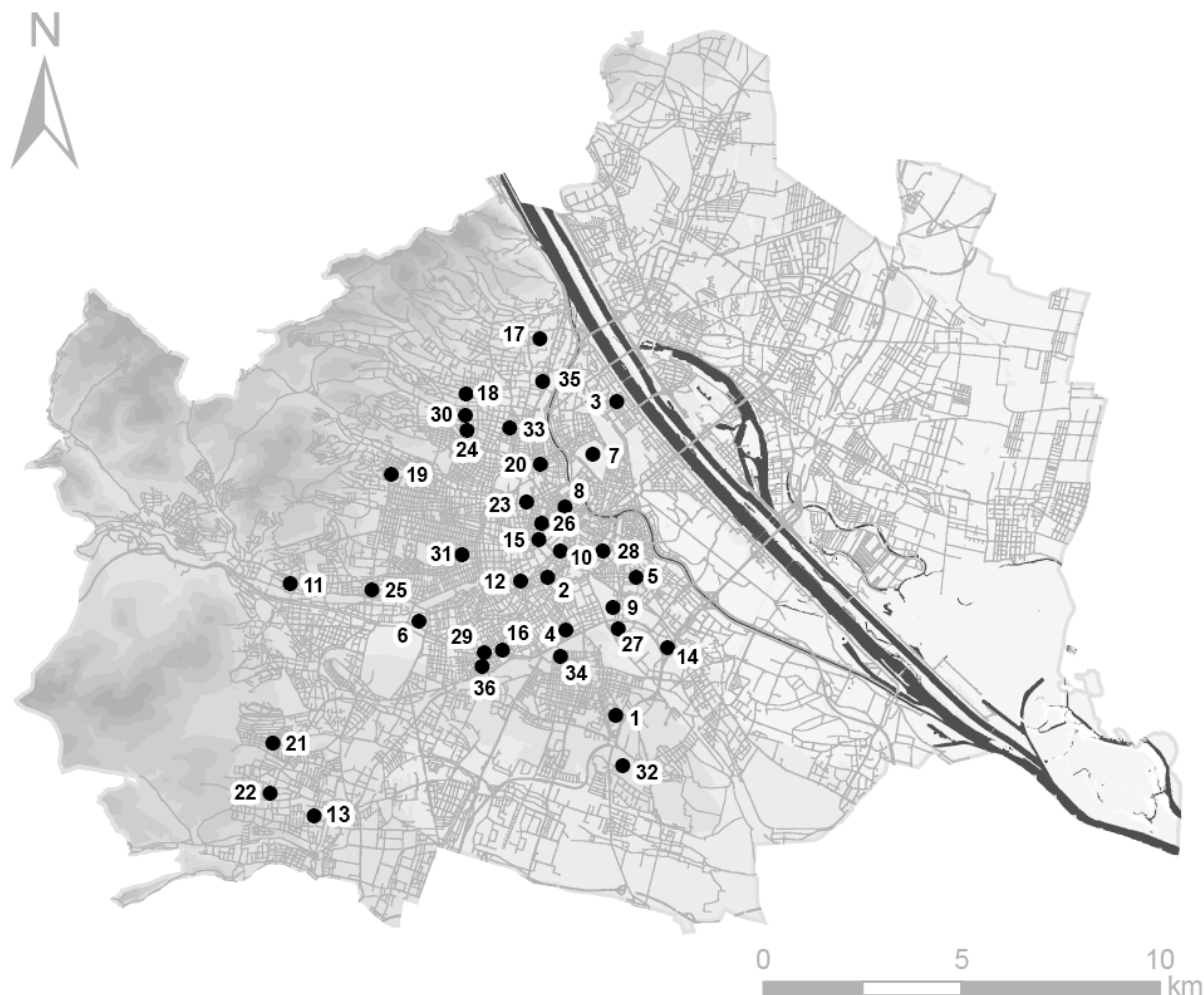


Figure 1. Centroids (black dots) of the 36 city parks where bird surveys were carried out. Dark grey lines of the Vienna relief map represent main water bodies, light grey lines the road network within the city. Numbers refer to city park codes listed in Table 1.

Bird surveys

Between 2005 and 2017 each city park was visited nine times during winter months (December 2005, November 2008, January 2009, December 2009, December 2012, January 2013, December 2013, January 2015, January 2017). Bird surveys were carried out between 07:50 and 16:10 under favorable weather conditions, avoiding windy days and/or days of heavy rain or snowfall. Sampling effort was standardized according to park size (10 min per 1 ha). The existing network of paths and roads within a park was used for survey routes, trying to cover the entire area of the park in a zigzag-manner. Each bird species as well as the number of individuals per species heard or seen were recorded (except for over-flying birds), trying to avoid double-counts.

Predictor variables and response variable

Park area was calculated in ArcGIS 10.2 (ESRI) based on Vienna land use data of the year 2009 (City of Vienna 2018). The tree cover within each urban park was digitized in ArcGIS 10.2 (ESRI), using satellite images of the map service “ArcGIS Online basemaps” (0.3 m spatial resolution, date of origin: August 2011). Then – to attain the canopy heterogeneity within each city park – the perimeter of digitized canopy (m) was divided by the area of closed canopy (m²), defined as closed leaf cover tolerating gaps up to 5 m. Consequently, higher canopy heterogeneity values indicate a higher density of edges. For describing the connectivity of the 36 city parks in which bird surveys were carried out to other green spaces within the urban matrix, a network centrality measure was calculated (CA_{IDW}). CA_{IDW} considered

the distance (by applying inverse distance weighting) and the area of green spaces each city park was connected to. For quantifying CA_{IDW} not only the 36 city parks in which bird surveys were carried out were considered, but further 760 parks and other green spaces (meadows, lawns) using Vienna land use data of the year 2009 (City of Vienna 2018). High CA_{IDW} -values indicate a high area weighted connectivity of a city park to other green spaces within the urban matrix (Table 1).

To quantify food supply within each city park, only small Passeriformes weighing between 15 and 250 g were considered, as these birds are commonly preyed upon by Eurasian Sparrowhawks (Selås 1993). Information on weight for each species was extracted from the CRC handbook of avian body masses (Dunning 2008). To standardize prey availability for differences in park size, the mean number of small Passeriformes surveyed between November 2008 and January 2017 was divided by park area (measured in hectare). Furthermore, also the mean number of artificial food supplies per ha – as an indirect surrogate for prey density – was calculated. Therefore, in December 2013, January 2015 and January 2017 the number of food supplies such as bird feeders, bird fat balls and sites providing supplementary food on the ground were counted during field work.

During the 324 (36 city parks x 9 surveys per park) bird surveys conducted only small numbers of Sparrowhawks (min: 0, max: 2, mean \pm standard deviation: 0.08 ± 0.31) could be observed. Hence, to avoid zero-inflated models (see below), we pooled the nine surveys and used binary (presence-absence) data as response variable for all further analyses. A city park was assigned “0” if no Sparrowhawk could be observed during the nine surveys and “1” if the species could be observed at least in one of the nine surveys.

Statistical analysis

To facilitate the interpretation of effect sizes all predictor variables were mean centered and standardized [(raw value – mean)/standard deviation] prior to analyses (Schielzeth 2010). To test for effects of park area, canopy heterogeneity, CA_{IDW} and density of prey and bird feeders on the occurrence of Eurasian Sparrowhawks Generalized Linear Models (GLMs; with binomial error distribution and logit-link function) were carried out. As the calculated Pearson correlation could indicate a very weak negative relationship between prey density and park size ($r = -0.289$, $p = 0.086$), perhaps as edges of urban green spaces attract particular high numbers of birds (e.g. flocks of House Sparrows *Passer domesticus*) from adjacent highly sealed areas, we also included the interaction term prey density and park size in our models. In contrast, no relationship existed between prey density and feeder density (Pearson correlation: $r = 0.058$, $p = 0.738$). GLMs were ranked using Akaike's information criterion corrected for small sample sizes (AIC_c) as the sample size divided by the number of parameters included in the models was < 40 (Symonds and Moussalli 2011). Only models that had an AIC_c difference (ΔAIC_c) < 4 from the best model (= model with lowest AIC_c value) were included in the candidate set (Burnham et al. 2011). To minimize multi-collinearity models containing two or more strongly correlated predictor variables ($r \geq 0.4$) were discarded from the candidate set.

For these best ranked models Akaike weights (= the relative likelihood of the model being the best) were calculated. Furthermore, for each predictor variable included in the best ranked models its relative importance (= sum of Akaike weights over all the models in which the variable appears) was evaluated.

Statistical analyses were carried out in R 3.0.3. (R Core Team 2014), using the R package glmulti (Calcagno 2013) and MuMIn (Barton 2016).

As park size proved to be of prime importance for the occurrence of Sparrowhawks in city parks (see results section), we finally calculated a logistic regression describing the likelihood of occurrence in relation to park size.

Results

Of the 36 city parks considered in this study, 14 parks were occupied by Sparrowhawks, whereas the species was not observed in 22 parks. When testing for effects of city park characteristics on the occurrence of Sparrowhawks, park size, prey density and the interaction term were included in all three best ranked models (Table 2). The null model was ranked 27th among the 47 candidate models. CA_{IDW} and feeder density were of minor importance in explaining the probability of Sparrowhawk occurrence (Table 2, Table 3). Canopy heterogeneity wasn't included in the best ranked models. Both, park area and prey density, and the interaction between these two explanatory variables proved to have a positive effect on Sparrowhawk occurrence (Table 3).

Table 2. Best ranked models ($\Delta AIC_c < 4$) explaining the occurrence of Sparrowhawks in Vienna city parks. For all included variables the relative importance is provided. Furthermore, Akaike's information criterion corrected for small-sample bias (AIC_c), differences in AIC_c values of each model compared with the model with the lowest AIC_c value (ΔAIC_c), and the Akaike weights (ω_i) are listed. Black dots indicate variables included in the respective model.

Predictor variable	1	2	3	Relative importance of variable
Park area	•	•	•	1
Park area x prey density	•	•	•	0.89
Prey density	•	•	•	0.85
CA_{IDW}		•		0.3
Feeder density			•	0.22
AIC_c	29.69	31.59	32.17	
ΔAIC_c	0	1.9	2.47	
ω_i	0.47	0.18	0.14	

Table 3. Full model averaged estimates of parameters explaining the occupancy of Vienna city parks by Sparrowhawks. Estimates whose confidence intervals (CI) do not contain zero are printed in bold.

Predictor variable	Estimate	SE	Adjusted SE	95 % CI
Intercept	1.9	1.51	1.55	-1.11 – 4.97
Park area	8.42	3.94	4.04	0.51 – 16.34
Prey density	5.27	3.47	3.55	0.27 – 12.1
Park area x prey density	8.61	5.24	5.36	0.61 – 18.83
CA_{IDW}	-0.18	0.45	0.46	-1.95 – 0.73
Feeder density	0.07	0.38	0.39	-1.22 – 1.86
Canopy heterogeneity	-0.01	0.12	0.13	-1.41 – 0.72

The 50 % threshold for Sparrowhawk occurrence in city parks described by a logistic regression ($\chi^2 = 21.14$, $p < 0.001$) was at a park size of ca. 5 ha (Fig. 2). While Sparrowhawks were recorded in 71.4 % of parks larger than 5 ha ($n = 14$), the species was only recorded in 18.2 % of parks smaller than 5 ha ($n = 22$).

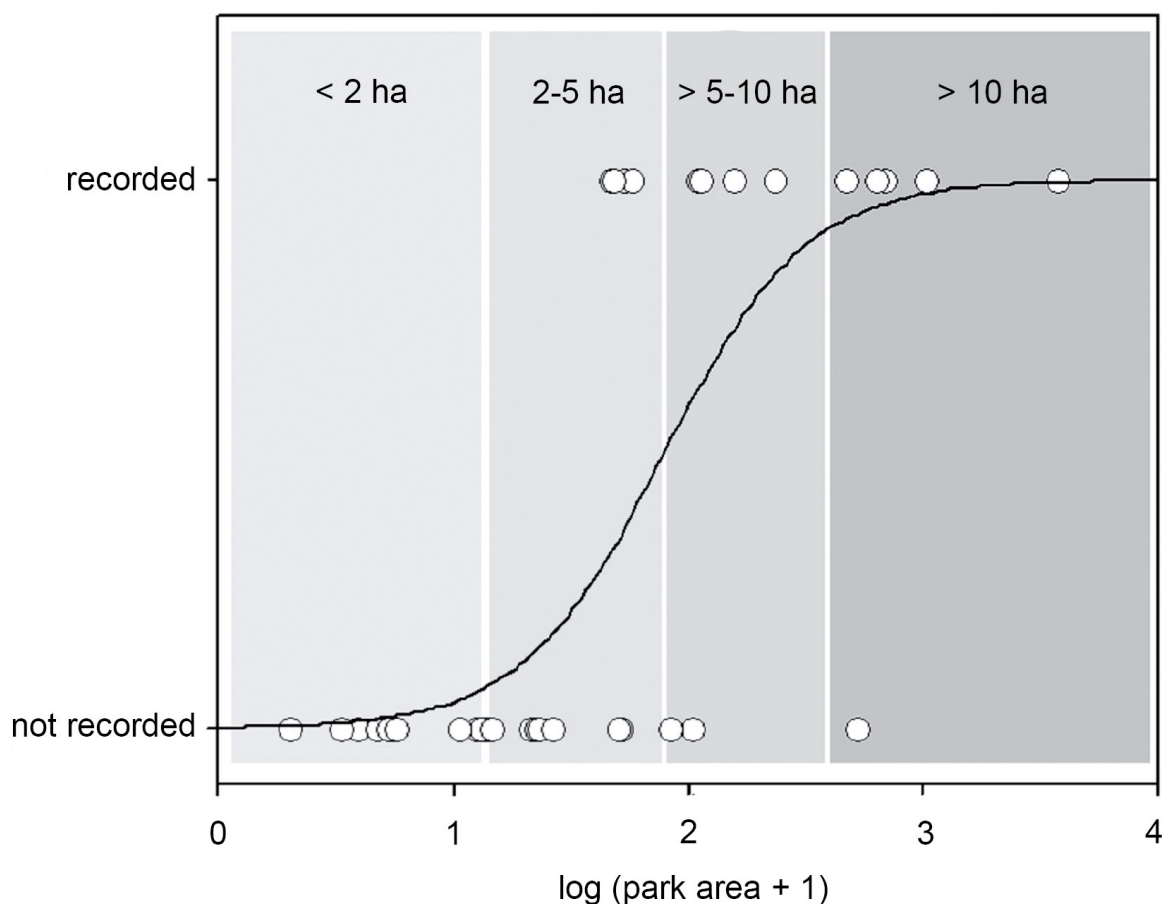


Figure 2. Logistic regression describing the likelihood of Sparrowhawk occurrence in relation to park area. To improve the fit to normality park size was $\log(x + 1)$ -transformed.

Discussion

According to our results park size, prey density and the interaction term of both variables proved to be of major importance in explaining the winter occurrence of Sparrowhawks in city parks. Larger parks showed a higher probability of park occupancy by this woodland raptor species than smaller ones. Woodlots embedded in an urban landscape generally experience higher levels of human disturbance compared to rural forests (Kang et al. 2015). Furthermore, in small patches negative effects of disturbance are increasing due to higher edge/area ratios and consequently the proportion of undisturbed core areas decreases (Fernández-Juricic 2000; Fernández-Juricic 2001). Although Eurasian Sparrowhawks increasingly represent successful city-dwellers (Newton 2010; Papp 2011), they still show greater levels of fear towards the proximity of humans than do most passerine species (Møller 2012). Consequently, they still avoid nesting close to human habitation even in urban environments (Abe et al. 2007). Moreover, more aggressive nest defense behavior of female Eurasian Sparrowhawks towards approaching humans within urban habitats is indicative of higher stress level compared to rural conspecifics (Kunca and Yosef 2016). Human disturbance may also negatively affect habitat quality for Sparrowhawks in winter, resulting in a preference for larger city parks. There this small

woodland raptor has more opportunities to find undisturbed spots for roosting, plucking and resting, representing important habitat requisites (Ortlieb 1995).

Higher prey density has already been suggested as a key factor for higher breeding success of Eurasian Sparrowhawks in urban than in rural environments (McGrady 1991; Thornton et al. 2017). During winter, urban areas may have a greater abundance of small birds due to the intense provisioning of supplementary food at bird feeders (Jokimäki and Suhonen 1998; Fuller et al. 2008). However, as it has already been found for the closely related Sharp-Shinned Hawk, these predictable “prey hotspots” are not necessarily highly attractive for hunting Sparrowhawks (Roth II and Lima 2007). This is also emphasized by our study. Although prey density was an important predictor for the occurrence of wintering Eurasian Sparrowhawks in city parks, feeder density was of minor importance. Small birds show highly effective defense mechanisms. Hence, just a tiny fraction of the birds that a hunting hawk encounters can be attacked with any chance of success, and even then potential prey usually detects the hawk in time to escape (Newton 2010). Additionally, Passerines in high densities, or aggregating close to bird feeders, benefit from a reduced predation risk due to foraging in flocks. Among others this reduced predation risk may arise from a reduced ability of the confused predator to single out and attack individual prey and increase the probability of the predator being detected (Sridhar et al. 2009). Consequently, to increase the proportion of successful hunting attempts Eurasian Sparrowhawks and other *Accipiter* species seem to select their prey rather on the basis of vulnerability than on abundance (Cresswell 1996; Götmark and Post 1996; Roth II et al. 2006; Roth II et al. 2008). Thereby, solitary passerine birds foraging on the ground far from cover are easy prey for hunting *Accipiter* species (Cresswell 1996; Götmark and Post 1996; Roth II et al. 2006).

The two predictor variables prey density and feeder density were not related. Hence, maybe habitat structures providing shelter and food for Passerines are more important. For example, small areas with a structurally diverse woody understory, e.g. consisting of shrubs developing fruits or berries with bird-dispersed seeds in winter, can be highly attractive patches in city parks for (at least partly) frugivorous songbirds (e.g. thrushes such as Blackbird *Turdus merula*, Fieldfare *Turdus pilaris*, Redwing *Turdus iliacus*; pers. observation). Measures improving the habitat structure of city parks can easily be implemented, thereby enhancing habitat quality for birds wintering (and breeding) in urban areas.

As already shown for the Northern Goshawk (*Accipiter gentilis*) built-up areas can provide profitable hunting grounds (Rutz 2003; Rutz 2006). Hence, city parks surrounded by a low number of green spaces might not indicate limited access to suitable hunting grounds for Eurasian Sparrowhawks. As a consequence, the extent of green space connectivity only weakly influenced the occurrence of this species during winter in our study area.

According to our results the density of edges, facilitating the availability of perches along the margin of patches covered by trees, didn't explain city park occupancy by Eurasian Sparrowhawks. In urban environments raptors not only perch in trees but increasingly use anthropogenic structures such as electricity pylons, TV aerials or buildings (Rutz 2003; Rutz 2006). Additionally, concealment during hunting can not only be achieved by using well-hidden perches. In the course of contour-hugging flights *Accipiter* species fly fast and low above the ground, even using habitat structures such as cars and fences as visual obstructions (Rutz 2006; Newton 2010).

Conclusions

Predatory birds can be crucial for maintaining ecosystem functions (Sekercioglu 2006). Hence, promoting and preserving this functional group should be of high conservation concern especially within the urban landscape, already heavily suffering from functional homogenization (McKinney 2006; Devictor 2007). Several studies have already demonstrated the high ecological value of large city

parks to promote and preserve avian biodiversity within urban landscapes (Nielsen et al. 2014; Kang et al. 2015; Schütz and Schulze 2015). Also the results of our study on the Eurasian Sparrowhawk underline the importance of large semi-natural habitat fragments embedded in a human-dominated landscape. However, Sparrowhawk occurrence was not only positively related to park size, but was also positively affected by prey density and even more strongly by the interaction between both variables. Hence, it is not only important to maintain large green spaces within urban areas but also to maintain park structures maintaining high density of passerines.

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and materials

The dataset used and analysed during the current study is available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

Both authors conceived and designed the study, carried out bird surveys and analyzed the data (CS: model selection, CHS: logistic regression). CS drafted the manuscript. CHS read and approved the final version of the manuscript.

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2.4. A comparative evaluation of multi-resolution night-time satellite imagery as integrative measure for ecological impact assessment in urban areas

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Abstract

Urbanisation and anthropogenic impact are increasingly seen as major drivers of biodiversity loss in a world of rapid urban growth. For ecological research purposes, quantifying the degree of urbanisation and associated factors within city borders is challenging due to the complex interactions between social, economic and environmental variables in urban ecosystems. In this paper, we examine the potential of night-time satellite imagery as a tool to integrate the large set of urbanisation metrics into a single variable for assessing potential adverse impacts of urbanisation on avian diversity within city parks. In addition to serving as proxy for human-related effects artificial light at night represents a direct threat to ecosystems, referred to as ecological light pollution. The use of public coarse-resolution night-time imagery for light pollution studies has been successfully demonstrated. We explore the applicability of commercial very high resolution night lights data from the EROS B satellite in comparison to the widely used coarse public data from the VIIRS sensor. This allows for a detailed assessment of local spatial configuration patterns of light pollution, going beyond previous applications that used regional average light intensity as proxy for urbanisation parameters. Additionally, park area and built-up area ratios in park surroundings are included in the analysis, accounting for previously demonstrated impact on avian diversity. Bird data for 36 city parks in the study area of Vienna, Austria, were collected in surveys carried out between 2009 and 2015. Results reveal that urbanisation metrics based on night-time imagery indicate adverse effects on bird diversity, with high levels of light pollution causing decreasing numbers of bird species. Both coarse and very high resolution night lights data represent value in explaining bird diversity changes, with the coarser VIIRS data unexpectedly showing higher statistical significance. Night-time satellite data outperforms land use data in assessing changes in avian diversity in terms of statistical explanatory power. We conclude that integration of multi-resolution satellite-derived night-time light data is a promising approach for assessing anthropogenic impact and associated ecological consequences in complex urban environments and recommend further research in that domain.

Keywords

Bird diversity, city parks, satellite night-time light data, EROS B, very high resolution, light pollution

Own contribution

Study design: 30 %, Data collection: 50 %, Statistical analyses: 100 %, Manuscript preparation: 60 %

Introduction

Due to ongoing urban development natural habitats, agricultural land and managed forests are increasingly replaced by built-up areas (Niemelä et al., 2011). Remnants of semi-natural vegetation then become visible as green patches in the urban matrix, differing in size, shape and isolation degree (Niemelä et al., 2011). Among these patches of green space, city parks satisfy the growing demand of citizens to stay in close touch with nature as well as aesthetic preferences for scenic beauty, cleanliness and pleasant sounds (Matsuoka and Kaplan, 2008). Furthermore, urban parks lower the albedo of metropolitan surfaces and therefore reduce heat island effects, they filter urban atmospheric pollutants such as carbon dioxide and can be used as a noise abatement (Forman, 2014; Niemelä et al., 2011). But most of all these spots of nature are strongholds of biodiversity in urban areas (Alvey, 2006; Cornelis and Hermy, 2004). As urbanisation is a major force of biodiversity loss and biological homogenisation (Concepción, et al. 2015; McKinney, 2006), promoting and preserving species diversity within city parks is an effective way to decelerate rapid biodiversity loss in our urbanising world (Alvey, 2006).

Empirical research focusing on the patterns and processes that affect biodiversity of urban green spaces provide evidence that species diversity of communities inhabiting these patches is predominantly determined by park size. Thereby, large parks show higher taxonomic and functional diversity compared to smaller ones due to increasing habitat diversity and microhabitat heterogeneity (Cornelis and Hermy, 2004; Nielsen et al., 2014; Schütz and Schulze, 2015). To a smaller extent species diversity may also be related to the permeability of the urban matrix adjacent to each city park (Nielsen et al., 2014). To quantify the urbanisation degree of the landscape surrounding the city parks, the proportion of built-up and paved (i.e. 'sealed') areas is often used in ecological studies (Hahs and McDonnell, 2006; McIntyre et al., 2000). Within the urban landscape patches of sealed and unsealed land cover are mixing up. Hence, also landscape metrics describing the configuration of these habitat patches within the urban matrix such as total edge length between patches or patch richness may be essential when quantifying urbanisation (Hahs and McDonnell, 2006). Moreover, human activities in cities are often very intense, causing severe disturbance regimes. Consequently, demographic measures such as human population density or size of households are also important urbanisation metrics from an ecological point of view (Hahs and McDonnell, 2006; McIntyre et al., 2000). All these different facets of urban development processes should be considered in ecological studies as urban ecosystems are characterized by complex interactions between social, economic and environmental variables (Alberti, 2005). However, the large amount of potential variables for quantifying urbanisation intensity makes the selection of an appropriate subset of variables that best captures the variability in the landscape of interest challenging (Hahs and McDonnell, 2006). Furthermore, finding the most informative combination among available urbanisation measures is often limited due to the high correlation between these interacting variables (Hahs and McDonnell, 2006).

In the study presented in this paper we examine the potential of satellite-derived night-time light data as a tool to integrate the large set of urbanisation metrics into a single variable for assessing anthropogenic impact and its associated consequences on biodiversity. The extensive use of low and moderate spatial resolution night-time light imagery over the last two decades for monitoring urban dynamics has shown a relationship between light brightness and demographic as well as economic variables (Elvidge et al., 1997; Ghosh et al., 2010; Ma et al., 2014; Shi et al., 2014). In addition to considering light patterns as proxy measure for urbanization, direct adverse effects of artificial light at night have long been evaluated in the scientific community, widely labelled as ecological light pollution when referring to environmental impacts (Rich and Longcore, 2006). Satellite night light data have consequently been proven to be useful tools in the conservation management and monitoring of single

species and whole ecosystems (Aubrecht et al., 2010a, b; Rodrigues et al., 2012; Mazor et al., 2013; Weishampel et al., 2016; Hu et al., 2018). In the presented study, remotely sensed night-time light data is evaluated to bridge the gap between complex inner-urban patterns of anthropogenic activity and conservation issues. We examine if light pollution data proves useful in evaluating adverse urbanisation effects on avian biodiversity in city parks. Birds represent excellent indicators to test for impacts on ecosystems associated with urbanization as they respond rapidly to changes in landscape configuration and composition (Alberti, 2005).

Unlike earlier studies that evaluated light pollution effects at broad geographical scales due to the limited spatial resolution of openly available nightlights data, we evaluate commercially acquired very high resolution (VHR) imagery as input for analyses at the scale of single city parks. In line with the above described urbanization impact theory, the hypothesis for this study is that city parks showing high light pollution within their borders or being surrounded by highly light-polluted habitats may show lower species numbers. By contrast, dark areas within park borders or in close vicinity may indicate near natural habitats, promoting avian diversity because of lower disturbance levels.

To address the challenge of variable selection, we further investigate if night light data remains an important predictor for species diversity when the two additional variables ‘park size’ and ‘proportion of sealed area surrounding each city park’ are considered. These two variables have already been proven to be major forces in shaping species richness of bird communities inhabiting city parks (Schütz and Schulze, 2015).

By using night-time light images as proxy measure for urbanisation, different aspects of urbanisation would be incorporated into a single, standardised variable, allowing for easier comparison between cities. Furthermore, due to advances in satellite technology these measures are not restricted any longer to regional or global scales, but can also be implemented at the local level. This is expected to enhance our understanding of urbanisation gradients as well as the ecological knowledge we can derive from them.

Study area and data

Study area

The study was conducted in Vienna (48°13' N, 16°22' E), the capital city of Austria located at the north-eastern extensions of the Alps. A total of 210 km² (51 %) of the city area is permanently covered by vegetation such as trees, shrubs and meadows. Around 44 % of the urban area consist of sealed area, mainly deriving from built-up areas and infrastructure facilities (Berger and Ehrendorfer, 2011).

Bird data

Bird surveys were carried out once a month in January 2009, December 2009, December 2012, January 2013, December 2013 and January 2015 in 36 city parks, ranging from 0.4 ha to 34.5 ha in size. Survey teams on average consisted of at least one experienced field ornithologist, assisted by three additional observers. Each park was surveyed between 07:50 and 16:20 under good weather conditions (i.e., avoiding windy days and/or days of heavy rain and snowfall, respectively). Sampling effort was standardised according to park size (10 min per 1 ha). The existing road network within a park was used for survey routes, trying to cover the entire area of the park in a zigzag manner. All species and the number of birds heard or seen were recorded (except overflying birds), trying to avoid double counting as effectively as possible. Waterfowls and birds with a strong affiliation to water (e.g., Grey Wagtail *Motacilla cinerea*) were excluded from further analyses as their occurrence is strongly driven by the presence of suitable waterbodies.

Light pollution data

Publicly accessible night-time light satellite data from the Visible Infrared Imaging Radiometer Suite (VIIRS) aboard the joint NASA/NOAA Suomi National Polar-orbiting Partnership (NPP) mission were obtained from the website of the NOAA National Centers for Environmental Information (NOAA, 2018). VIIRS night-time lights are generated using the sensors' day/night band (DNB) operating at a spectral range of 500-900 nm highly sensitive to very low levels of visible light (Liao et al., 2013; Miller et al., 2013). Until data from Suomi NPP became available operationally in early 2012 the only public source of satellite derived night-time lights imagery was the Operational Linescan System (OLS) aboard the satellites of the Defense Meteorological Satellite Program (DMSP). The accessible DMSP-OLS archive of processed night-time lights data reaches back to 1992 providing annual composites that reflect average stable lights as identified in nightly acquisitions over the course of a year (Elvidge et al., 2001). OLS data has been widely used for light pollution assessments, starting with characterization of sea turtle nesting areas in the early stages (Salmon et al., 2000). As compared to OLS night-lights data, the newer VIIRS data have improved in multiple ways, i.e. in terms of spatial resolution, dynamic range, quantization and saturation, on-board calibration, and the availability of spectral bands suitable for discrimination of thermal sources of light emissions (Elvidge et al., 2013; Jing et al., 2016). For urban area analytics, particularly the higher spatial resolution (750 m compared to a 2.5 km ground sampling distance for OLS) and the lack of unfavourable saturation effects in bright city cores are highly beneficial. VIIRS night light products are provided by NOAA as gridded 15 arc-second (~ 380 m for the case study area) monthly composites. We chose the March data set for the presented analysis after comparison with other monthly composites due to better data reliability inferred from the higher number of cloud-free observations used for the compositing process (this selection approach follows Aubrecht and León Torres, 2016).

The scientific community has been advertising the need for satellite sensors generating high resolution night-time imagery since the mid-2000s, e.g. with the proposed US Nightsat (Elvidge et al., 2007) and the European NYX (Arnoux and Aubrecht, 2013) mission concepts. To date, however, the only space-based sensor providing VHR night-imagery is the commercial Israeli Earth Remote Observation Satellite (EROS B). There are very few studies in the literature using EROS B in an environmental context. However, Levin et al. (2014) concluded that its fine spatial resolution imagery opens new avenues for studying urban light pollution. EROS B has been operational since 2006 providing panchromatic imagery at 70-80 cm resolution (depending on acquisition mode). The satellite is operated by ImageSat International (ISI) which handles tasking and quality assurance of on demand image acquisition (ISI, 2016). Due to high manoeuvrability EROS satellites can be pointed to sites of interest on nadir or at oblique angles (< 45 degrees) which allows image acquisition anywhere on Earth as often as three times per week. For the presented study, two EROS B image scenes were tasked for the nights of April 18th and April 23rd 2015 to ensure full coverage of all 36 city parks where bird surveys had been carried out (plus a 500 m buffer around each park). The two scenes cover an area of 150 km² at a spatial resolution of 76 cm. Acquisition took place at 23:44 (April 18th) and 23:51 (April 23rd) local time respectively pointing approximately 25 degrees off nadir, with 0 % cloud cover recorded on both nights. ImageSat International eventually delivered radiometrically (Level 1A) and geometrically (Level 1B) corrected image products. Minimal post processing included correcting georeferencing and filtering for noise and other artefacts.

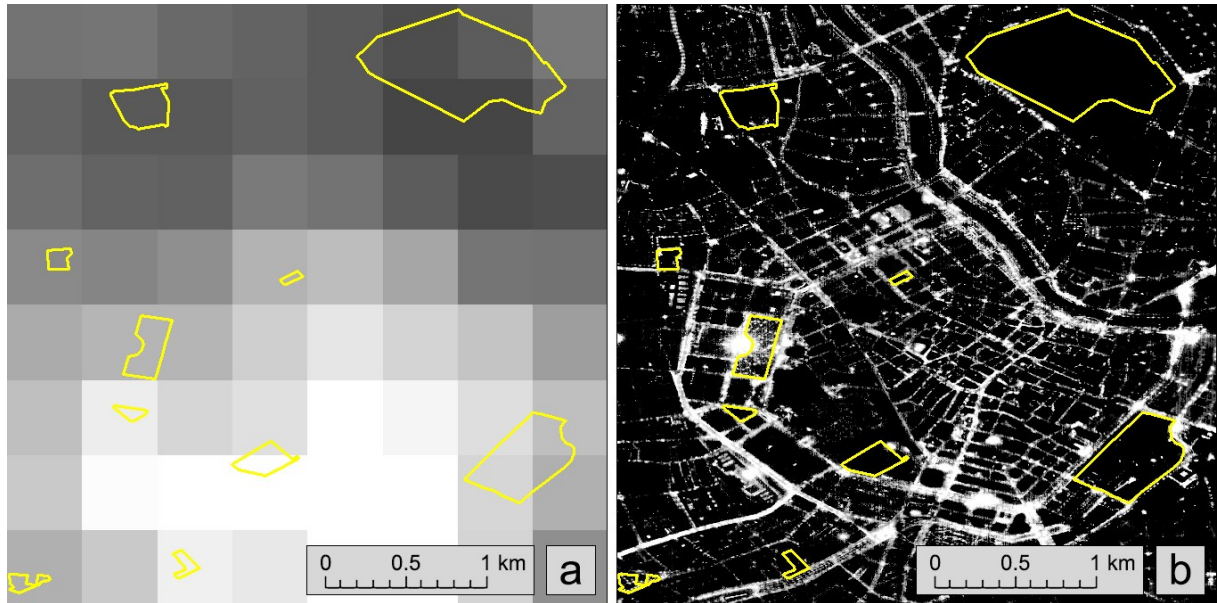


Figure 1. Overview of Vienna city centre with ten parks (polygons with yellow outlines) considered in this study overlaid on night-time light data derived from: (a) NNP-VIIRS imagery of March 2015; (b) EROS B imagery of April 2015. Dark areas indicate low levels of brightness; highly lit areas appear in bright grey and white tones.

Methods

Quantification of urbanisation metrics derived from night light data

The impact of the light pollution on the environment is complex and our understanding of the full range of ecological consequences still limited. However, while not the only ecologically relevant measure, most studies evaluating such impact consider amount (intensity) and duration of light pollution as most important parameters (Longcore and Rich, 2004). In order to assess average lighting intensity as detected by both sources of night-time light data, we use zonal statistics (ESRI ArcGIS) to calculate mean brightness within the borders of city parks in our study area (variables labelled ‘VIIRS park’, ‘EROS B park’) and within a buffer of 100 m surrounding each city park (variables ‘VIIRS buffer’, ‘EROS B buffer’).

To go beyond average brightness measures and fully exploit the very high spatial resolution of the EROS B data, additional hot spot statistics (Getis-Ord G_i^*) are calculated to identify areas where pixels of either irregularly high (hot spots of light pollution) or low brightness values (cold spots of light pollution) cluster spatially within the parks or the buffer areas. To describe shape characteristics of hot spot and cold spot areas the indices Solidity (SOLI) and Square pixel metric (SqP) were used, which have already been proven as reliable measures in characterizing the complexity of land use classes in remote sensing imagery (Frohn, 2006; Jiao and Liu, 2012). Thereby, the SOLI index was slightly modified for our analyses (SOLI_{mod}). Whereas SOLI compares the area of a polygon to the area of the convex hull surrounding the polygon (Jiao and Liu, 2012), SOLI_{mod} compares the area of a hot spot or a cold spot polygon to the area of the city park polygon or the buffer polygon. For example, SOLI_{mod} for the hot spot patch within a city park is calculated according to the following formula:

$$\text{SOLI}_{\text{mod}} = A/A_{\text{park}}$$

where A is the area of the hot spot and A_{park} is the area of the park polygon. SOLI_{mod} values for polygons with no holes are 1.0 and values for concave polygons are smaller than 1.0 (Jiao and Liu, 2012).

SqP is a perimeter-to-area shape complexity metric:

$$\text{SqP} = 1 - (4 * A^{1/2})/P$$

where P is the perimeter of a hot spot or a cold spot patch, and A is the area of a hot spot or a cold spot patch. SqP values reach 0 for a square patch and approach 1 as patches become more complex (Frohn, 2006).

To account for potential amplification factors we also calculate an integrative light index in addition to the separate mean brightness and complexity parameters. Our hypothesis, based on ecological light pollution theory, is that while mean brightness is the dominant aspect of light pollution, complexity of brightness patterns (within city parks and their surroundings) becomes an increasingly important factor for the suitability of avian habitats in generally brightly illuminated parks. The expectation is that birds would not yet abandon parks with generally high levels of light pollution in case internal less-lit refugium areas existed due to peak light distribution clustering. Hence, for our light index we weight the importance of mean brightness as minimum 50 % with the complementary weight assigned to internal patch complexity. Ranked average park brightness thereby defines the extent to which complexity patterns are contributing to the index composition. The brighter the park the stronger its internal and surrounding light complexity patterns are weighted in the index. For the brightest park, therefore, patch complexity is given the maximum 50 % weight, while for the darkest park patch complexity is not considered as a contributing element (mean brightness then considered as sole factor).

Quantification of urbanisation metrics derived from land use data

As indicated in the introduction, empirical evidence points at the dominant importance of ‘park size’ on biodiversity of urban green space. We therefore consider this as a comparative metric to variables derived from night-time lights data. Park area as well as the proportion of sealed area in a buffer surrounding each city park are calculated based on Vienna land use data from the period 2009 to 2012 (City of Vienna, 2018). Land use categories describing sealed areas (e.g. roads, buildings etc.) are merged and the proportion of sealed area within each 100 m buffer zone is calculated.

Statistical analysis

For a better fit to normality some variables are transformed (park size: $\log(x + 1)$; EROS B park, EROS B buffer: $\log(x)$). Afterwards, all predictor variables are mean centred and standardised $[(\text{raw value} - \text{mean})/\text{standard deviation}]$ prior to analyses to facilitate the interpretation of effect sizes (Schielezeth, 2010). To evaluate effects of 12 predictor variables (park size, sealed area, VIIRS park, VIIRS buffer, EROS B park, EROS B buffer, SqP park, SqP buffer, SOLI_mod park, SOLI_mod buffer, light index park, light index buffer) on avian species diversity of Vienna city parks, an information theoretic approach is applied. General Linear Models (GLMs) are ranked according to their information content determined by the Akaike’s information criterion corrected for small-sample bias (AICc). AICc is used as the sample size divided by the number of parameters included in models is < 40 (Symonds and Moussalli, 2011). All models that have an AICc difference (ΔAICc) < 2 are considered as best ranked (Burnham et al., 2011) and Akaike weights (= the relative likelihood of the model being the best; ω_i) for these models are calculated. For each parameter included in the candidate set of models the relative importance (sum of Akaike weights over all models in which the variable appears) is calculated. Averaging procedure is used to compute the average estimates of parameters included in best ranked models.

To minimize multi-collinearity, candidate models only consist of variables that are not strongly correlated ($r < 0.4$) according to Pearson’s Correlation Coefficient. All statistical analyses are carried out in R 3.0.3 (R Core Team, 2014), using the R packages ggplot2 (Wickham, 2009), glmulti (Calcagno, 2013) and MuMIn (Barton, 2016).

Results

Getis-Ord G_i^* statistics reveal significant cold spots only for the Rathauspark and its surrounding buffer. Significant hot spots are attained in the buffer polygons of every city park. Only two parks do not show significant hot spots within their borders. The largest hot spot area is found in the Schweizergarten, whereas the Ölzeltpark shows the smallest hot spot area (Figure 2).

Consequently, the metrics SOLI_mod, SqP and the light index are only calculated on the basis of significant hot spots. Further, the two parks Sternwartepark and Kongresspark are excluded from further analyses, as they do not show significant hot spots within their borders.

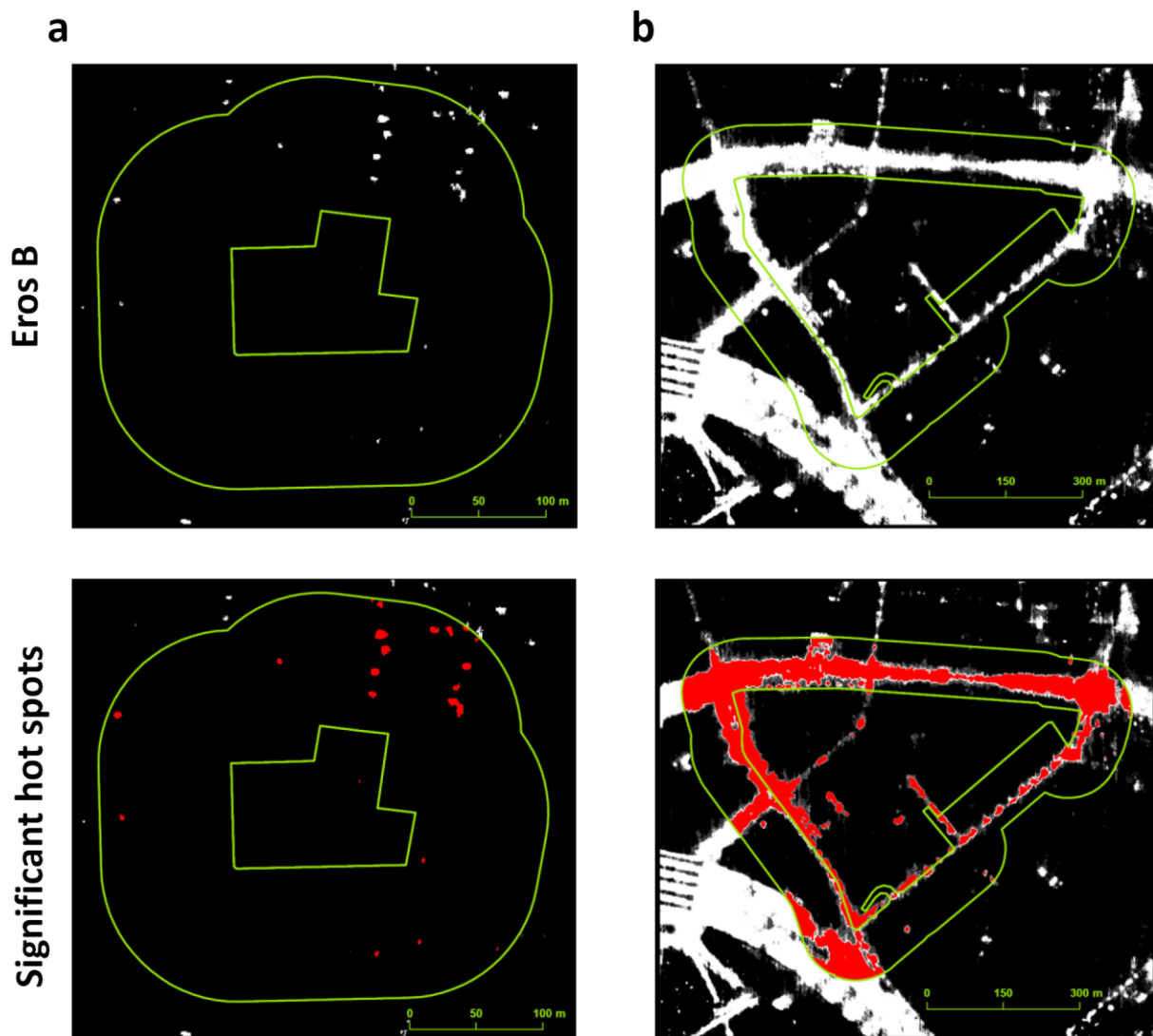


Figure 2. EROS B satellite images and significant hot spots (red polygons) derived from Getis-Ord G_i^* statistics for (a) Ölzeltpark and (b) Schweizergarten. Green lines indicate borders of the city parks and the 100 m buffer zone.

For predicting the number of recorded bird species in city parks of Vienna park size is of major importance. The variable is included in all four best ranked models, resulting in its relative importance of 1 (Table 1). Full model averaged estimates indicate a positive effect of park area on avian biodiversity (Table 2). Beside park area also the variables VIIRS buffer and VIIRS park are included in the best ranked models (Table 1). Thereby, increasing brightness values within city parks as well as in the urban matrix surrounding each city park lead to a decrease in avian species diversity (Table 2). SqP park is included in two of the best ranked models (Table 1). Thereby, increasing complexity of light pollution hot spots

within the park area positively affects species diversity (Table 2). All other metrics describing hot spot configuration as well as mean brightness values based on EROS B night-time light data and the proportion of sealed area do not statistically affect bird species diversity in Vienna city parks.

Table 1. The four best ranked models ($\Delta AICc < 2$) explaining the number of bird species recorded in Vienna city parks. Akaike's information criterion corrected for small-sample bias (AICc), differences in AICc values of each model compared with the model with the lowest AICc value ($\Delta AICc$), the Akaike weights (ω_i) and the relative importance (RI) of the variables included in the best ranked models are listed.

Predictor variable	1	2	3	4	RI
Park area	•	•	•	•	1
VIIRS buffer	•			•	0.39
VIIRS park		•	•		0.38
SqP park			•	•	0.28
AICc	172.01	172.06	172.81	172.83	
$\Delta AICc$	0	0.05	0.8	0.82	
ω_i	0.2	0.2	0.13	0.13	

Table 2. Full model averaged estimates of the intercept and the parameters included in the best ranked models to explain the recorded number of bird species in city parks of Vienna.

Predictor variable	Estimate	SE	Adjusted SE
Intercept	19.06	0.48	0.5
Park area	6.67	0.59	0.61
VIIRS buffer	-1.43	0.55	0.57
VIIRS park	-1.44	0.55	0.57
SqP park	0.74	0.58	0.61

Discussion and conclusions

Park size represents the most important variable in explaining the number of bird species recorded in Vienna city parks as it is included in all best ranked models. Also other studies have already shown that an increase of park area positively affects the taxonomical diversity of bird communities (Nielsen et al., 2014; Schütz and Schulze, 2015). This species-area relationship is consistent with the predictions of the theory of island biogeography (MacArthur and Wilson, 1967), which is often applied in studies of avian communities inhabiting city parks (Fernández-Juricic and Jokimäki, 2001). Thereby, city parks and other green space remnants represent 'green islands' being isolated from the 'urban ocean' of built up structures and hence serve as the only suitable refuges for many bird species (Fernández-Juricic and Jokimäki, 2001; Nielsen et al., 2014). The positive relationship between park size and species number partly derives from larger parks showing greater habitat diversity and resource availability than smaller ones (Cornelis and Hermý, 2004; Fernández-Juricic and Jokimäki, 2001; Nielsen et al., 2014). Hence, the specific needs of forest and insectivorous bird species may only be satisfied in larger habitat patches (Fernández-Juricic, 2000). Additionally, large parks often have core areas that are unaffected by effects associated with habitat edges, such as higher levels of human disturbance. Consequently, beside edge specialist species – being highly habituated to human activities and showing high breeding densities at urban park edges – also species with specific habitat requirements can be found in the more undisturbed core areas (Fernández-Juricic, 2001).

In addition to confirming the impact of park size we are able to show correlation between internal city park characteristics and the recorded bird diversity by using mean brightness values from VIIRS night-time lights satellite data (averaged for individual parks). Thereby, increasing brightness values within city park borders cause decreasing numbers of bird species. Mean brightness values of the much higher spatial resolution EROS B night lights data, however, are not included in the best ranked models.

The light regime within city parks (that are not closed at night anyway) may be driven by the intent to enhance safety and security for the public at night (Posch et al., 2013), although there is no evidence that increased outdoor lightening would indeed prevent crimes (Steinbach et al., 2015). At the same time, authorities may more and more become aware of negative effects of light pollution on wildlife and ecosystems (Posch et al., 2013). Hence, lighting within city parks may partly or completely be turned off during the whole night or during certain hours because of ecological but also economic reasons (Posch et al., 2013; Steinbach et al., 2015). As a consequence, the very high-resolution EROS B night-time imagery may not reflect the daytime disturbance levels, thus potentially constraining its ability to describe integrative urbanisation effects on species diversity of city park bird communities. In contrast, VIIRS data pixels (featuring much coarser spatial resolution) commonly fail to accurately delineate park boundaries having mixed-content pixels that contain both park and surrounding area. Further adding the effect of sky glow prevalent in coarse-resolution night-time satellite imagery, i.e. distant light sources artificially elevating local brightness levels, makes it difficult to disentangle light pollution conditions within and outside city park borders. Hence, mean VIIRS-brightness values of city parks and buffer zones are highly correlated, with high values in both areas exerting negative effects on the species richness.

VHR EROS B imagery for the first time offers the possibility to describe patch geometry of light polluted fragments using satellite-derived measurements. In accordance with other studies that found that the shape of habitat patches structures bird communities of fragmented landscapes (Davis, 2004), also our results reveal that more complex-shaped light pollution hot spots within city parks positively affect avian diversity. Complex light polluted patches are closely interwoven with lesser polluted surroundings and hence, city parks then not only offer habitat to birds habituated to high levels of disturbance but also to habitat specialists longing for undisturbed areas.

Not only an increase of patch size but also high levels of patch connectivity, quantified by the presence of corridors or the distance between patches, can exert positive effects on avian biodiversity in fragmented landscapes (Martensen et al., 2008; Uezu et al., 2005). High urbanisation levels, leading to increasing distances between remnant habitat patches and decreasing numbers of vegetation corridors, negatively affect connectivity between city parks (Savard et al. 2000). Dispersal abilities of habitat specialist species, unwilling to move through the inhospitable urban matrix, may then decrease, reducing chances of park occupancy and hence local bird diversity (Fernández-Juricic, 2000). Indeed, several studies on bird communities have already shown that urban green spaces embedded in a highly urbanised landscape are negatively affected in their species richness (Ferenc et al., 2014; Ikin et al., 2013; Schütz and Schulze, 2015). In accordance with these findings, also in our study high levels of light pollution – indicating highly urbanised areas – in a 100 m buffer zone surrounding the city parks had negative effects on the species diversity. Thereby, VIIRS night-time light data appear to be reliable indices to quantify the permeability of the urban matrix. Together with park size VIIRS buffer is included in the best ranked model. VIIRS night-time light data have already been proven to quantify not only changes in land use, but also economic as well as demographic dynamics involved in urbanisation processes (Ma et al., 2014; Shi et al., 2014), making them useful tools to quantify the permeability of the urban matrix in the context of ecological studies.

Although having much higher spatial resolution than VIIRS data and thus giving a more detailed picture of internal city characteristics (Levin et al., 2014), EROS B data do not show statistical significance in representing the permeability of the urban matrix, neither by mean brightness values of the buffer area nor by shape characteristics describing patch geometry of fragments affected by light pollution. The results of our study reveal that night-time satellite imagery provide an alternative integrative measure of urbanization and thereby explain avian diversity better than the use of sealed area ratio, which is constraint to quantifying built-up area. We recognize that there are a multitude of other factors shaping avian biodiversity such as park age or specific habitat qualities within urban parks like native plant species richness or structure and complexity of woody vegetation (Fernández-Juricic, 2000; Nielsen et al., 2014). However, instead of identifying a subset of parameters describing the variance in avian biodiversity as completely as possible, our study focuses on the evaluation of the integrative potential of satellite night images in helping predict taxonomical diversity of bird communities. While effects of artificial light pollution on biodiversity are often overlooked (Mazor et al., 2013), we find that night lights derived from satellite imagery serve as significant determinants for the permeability of the urban matrix and hence the avian diversity inhabiting remnants of semi-natural vegetation. Unlike other environmental or anthropogenic parameters used for quantifying urbanisation gradients, night-time light data enable the incorporation of different facets of urbanisation into a single variable, drawing a clearer picture of economic and demographic processes that take place within the borders of a city.

This paper presents the first study evaluating commercial VHR night-time satellite data for quantification of ecological light pollution at the local inner-urban level. Approaches presented herein are experimental in nature given the lack of comparable analyses. While extremely detailed in its visual representation of brightness patterns, we conclude that our initial broad assumption that VHR commercial night lights imagery from EROS B would vastly outperform (in terms of biodiversity-related explanatory power) coarser-scale publicly available VIIRS data does not hold. The positive exception is the new and statistically relevant internal complexity parameter, only possible due to the high granularity of the VHR imagery. We see these results as a valuable first step towards better understanding the potential use of multi-resolution night imagery – a research domain practically still non-existent when compared to traditional daytime remote sensing analysis. Following preliminary elaborations of Katz and Levin (2016) who compared EROS B to ground based light brightness measurements, we recognize the very specific perspective provided by space-based observations. At that high spatial resolution experience with night-time satellite observation is very limited and further studies are needed to improve our understanding of technical characteristics and parameters across different application domains. In that context we would also like to resurface earlier requests of the scientific community for dekametre resolution night-time sensors (Elvidge et al., 2007, Arnoux and Aubrecht, 2013). Successful experience with airborne sensors and scale-smoothing experiments illustrate the usefulness of that resolution level (nested between the coarser VIIRS and finer EROS B data) for a variety of application areas and this might also apply to urban ecology issues. Furthermore, light brightness distribution and light pollution perception at the ground is influenced by a variety of factors other than upwards reflection mainly collected by a satellite sensor, including multi-directional reflectance and sensor sensitivity to low light levels especially in dark areas. In conclusion, we feel that the integration of satellite-derived night-time light data is a promising approach for future ecological studies in complex highly modified urban environments. However, open questions remain and we hope to stimulate further research in that domain.

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2.5. Der Effekt von Augengröße und Lichtverschmutzung auf den Aktivitätsbeginn von Vögeln im Wiener Stadtgebiet

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Schütz C. & C. H. Schulze: The effect of eye size and light pollution on daily activity patterns of birds in the city of Vienna.

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Abstract

In birds artificial light pollution can cause an earlier start of daily activity with a stronger response to artificial light in species that generally start their dawn song earlier. This is suggested to be related to interspecific variation in eye size. However, until now no study included these two variables in multivariate analyses to test for an additive effect of relative eye size (eye size adjusted for differences in body size) and artificial light pollution. That was realized in this study, also accounting for possible effects of varying temperature and season on the activity start of eleven common songbirds. To assess the activity start of bird species, point counts have been carried out between November 2014 and April 2015 at 84 randomly selected survey points within the city borders of Vienna. Birds were recorded 15 min before until 15 min after start of civil twilight. At survey points beside temperature also sky brightness as well as light intensity were measured every 15 min. For analyses light pollution was also quantified on a regional scale using VIIRS night-time satellite images. Data on birds' eye size derived from a personal database and from literature. Linear mixed-effects models indicate that large-eyed bird species tend to show an earlier start of their activity. While light pollution quantified on a local scale (census point) doesn't prove to strongly affect activity start of birds, effects are found when considering average light pollution within a buffer of 250 and 500 m around census points. If large-eyed species benefit disproportionately from light pollution, this could contribute shaping bird communities inhabiting urban environments.

Own contribution

Study design: 50 %, data collection: 90 %, statistical analyses: 100 %, manuscript preparation: 100 %

Einleitung

Ökologische Lichtverschmutzung – definiert als die Aufhellung des Nachthimmels durch (meist) künstliche Lichtquellen, welche die natürlichen Lichtverhältnisse in Ökosystemen verändert (Longcore & Rich 2004) – nimmt in Folge der steigenden Urbanisierung und dem kontinuierlich wachsendem Lebensstandard rapide zu (Gil & Brumm 2014; Kyba et al. 2017). Lichtverschmutzung ändert dabei die räumlichen, zeitlichen und spektralen Eigenschaften natürlicher Lichtverhältnisse und beeinflusst damit die Physiologie und das Verhalten einer breiten Palette an Organismen (Navara & Nelson 2007; Gaston et al. 2013; Dominoni et al. 2016).

Wie wir Menschen sind Vögel überwiegend tagaktive, vornehmlich visuell gesteuerte Lebewesen. Daher spielt Licht in ihrem Leben eine große Rolle und dementsprechend kann „falsches“ Licht zur falschen Zeit am falschen Ort fatale Auswirkungen haben (Hüppop et al. 2013). So wurden bei nachts ziehenden Vögeln, die zum Navigieren u. a. den Sternenkompass nutzen (Berthold 2008), besonders in bedeckten Nächten anziehende Effekte hell erleuchteter Strukturen in einer ansonsten dunklen Umgebung beobachtet (Hüppop et al. 2013). Diese Effekte können die Wahl des Rasthabitats und damit auch die Effizienz der Nahrungsaufnahme während des Zuges beeinflussen (McLaren et al. 2018). Aufgrund von Kursverlust und/oder Desorientierung kann eine derartige Lichtattraktion aber auch zu einem dramatischen Anstieg der Flugdauer und im schlimmsten Fall zur völligen Erschöpfung oder zur Kollision mit beleuchteten Strukturen wie Hochhäusern, Sendemasten oder Windkraftanlagen führen (Hüppop et al. 2013; Van Doren et al. 2017).

Im städtischen Umfeld, in dem künstliche Lichtquellen einen permanenteren und gleichmäßiger verteilten Charakter zeigen, üben sie weniger anziehende Effekte aus, sondern verursachen vielmehr Verschiebungen in den tageszeitlichen und saisonalen Aktivitätsmustern von Vögeln (Gaston et al. 2013; Gil & Brumm 2014; Da Silva et al. 2015). Nächtliche Beleuchtung löst beispielsweise einen früheren Aktivitätsbeginn aus, wobei dieser Effekt bei jenen Vogelarten besonders stark ausgeprägt ist, die ihren morgendlichen Gesang in Relation zum Sonnenaufgang sehr früh beginnen (Kempenaers et al. 2010; Russ et al. 2015). Grund hierfür könnten zwischenartliche Unterschiede in der relativen Augengröße und damit in der unterschiedlichen visuellen Leistungsfähigkeit unter geringen Lichtintensitäten sein. Untermauert wird diese Annahme durch Studien, die einen negativen Zusammenhang zwischen Augengröße und morgendlichem Aktivitätsbeginn zeigen (Thomas et al. 2002; Ockendon et al. 2009).

Im Rahmen dieser Studie sollen nun zum ersten Mal die beiden maßgeblichen Prädiktorvariablen Augengröße und Lichtverschmutzung – gemeinsam mit anderen potentiell bedeutenden Variablen wie Temperatur und Jahreszeit (Da Silva et al. 2014; Russ et al. 2015; Da Silva et al. 2017) – in multivariate Analysen integriert werden. Dadurch wird die Einflussstärke dieser beiden Variablen auf den Aktivitätsbeginn von Vögeln miteinander vergleichbar. Zudem basieren Studien, die den Effekt von Lichtverschmutzung auf den Aktivitätsbeginn von Vögeln untersuchen, überwiegend auf kleinräumigen Lichtverschmutzungsmaßen (Kempenaers et al. 2010; Russ et al. 2015; Da Silva et al. 2017). Neben punktuellen Messungen der Lichtverschmutzung, wird in dieser Studie Lichtverschmutzung auch auf Basis von Nachtlucht-Satellitenaufnahmen für großräumigere Flächen quantifiziert. Abseits von der Gesangsaktivität ist der Effekt von Lichtverschmutzung auf tägliche Aktivitätsmuster von Vögeln noch wenig untersucht (Gil & Brumm 2014). Unsere Studie berücksichtigt daher als abhängige Variable den allgemeinen Aktivitätsbeginn und ist überwiegend außerhalb der Brutzeit angesiedelt.

Material und Methoden

Untersuchungsgebiet und Vogelerhebungen

Die Freilandarbeiten wurden zwischen November 2014 und April 2015 in Wien an zufällig ausgewählten Punkten durchgeführt. Für die Zufallsauswahl wurde das Stadtgebiet in ArcGIS mit einem 1 x 1 km-Raster überzogen und für jede Rasterzelle die mittlere Strahldichte berechnet. Daten zur Strahldichte (Einheit: Nanowatt pro Steradian und pro Quadratcentimeter) stammen von VIIRS-Nachtlicht-Satellitenaufnahmen (NOAA 2018; Details siehe weiter unten). Anschließend wurde jede Rasterzelle einer der folgenden vier Gruppen zugeordnet: kaum lichtverschmutzt ($< 5 \text{ nW}/(\text{cm}^2 \cdot \text{sr})$), leicht lichtverschmutzt ($5,01\text{-}15 \text{ nW}/(\text{cm}^2 \cdot \text{sr})$), mäßig lichtverschmutzt ($15,01\text{-}25 \text{ nW}/(\text{cm}^2 \cdot \text{sr})$) und stark lichtverschmutzt ($> 25 \text{ nW}/(\text{cm}^2 \cdot \text{sr})$). Für jeder Gruppe wurden 20 bis 22 Zufallspunkte (kaum lichtverschmutzt: $N = 20$, leicht lichtverschmutzt: $N = 21$, mäßig lichtverschmutzt: $N = 21$, stark lichtverschmutzt: $N = 22$) ausgewählt, wobei nur jene Punkte berücksichtigt wurden, die möglichst einfach zugänglich waren (Abb. 1). Die Aktivität aller Vogelindividuen, die visuell und/oder akustisch an den Kartierungspunkten registriert wurden, wurde erfasst, sofern es sich um Nachweise innerhalb von 50 m um den Beobachtungspunkt handelte. Die Gesamterfassungszeit pro Punkt betrug 30 min, wobei sich diese von 15 min vor bis 15 min nach Beginn der zivilen Dämmerung erstreckte. Die morgendliche bürgerliche Dämmerung beginnt, wenn sich die Sonne 6° unter dem Horizont befindet und endet mit dem Sonnenaufgang. Während dieser Zeitspanne – unter Abwesenheit von Mondschein und/oder künstlicher Beleuchtung – ist die vorherrschende Helligkeit für das menschliche Auge gerade ausreichend, um große Gegenstände grob zu unterscheiden, Details sind nicht auflösbar (Geoscience Australia 2018). Der Beginn der zivilen Dämmerung wurde für jeden Kartierungspunkt unter <https://galupki.de/kalender/sunmoon.php> ermittelt. Alle 84 Punkte wurden in zufälliger Reihenfolge einmal im Untersuchungszeitraum aufgesucht. An den Untersuchungspunkten wurde zudem ab Beobachtungsbeginn alle 15 min die Temperatur gemessen.

Lichtverschmutzung

Die Lichtverschmutzung an den Kartierungspunkten wurde auf verschiedenen räumlichen Ebenen ermittelt. Auf lokaler Ebene wurde am Beobachtungspunkt mit einem Luxmeter (Voltcraft DT 8820, Einheit: lux) die Lichtintensität aufgenommen. Mit einem Sky Quality Meter (Unihedron SQM-L, Einheit: Magnituden pro Bogensekunde²) wurde zudem die Himmelshelligkeit in einem Raumwinkel von ca. 20° um die Zentralachse gemessen (Unihedron 2017). Je niedriger der Wert, der vom Gerät erhalten wird, desto höher ist die Helligkeit des Nachthimmels und damit die Lichtverschmutzung (Posch et al. 2013). Eine Abnahme um $5 \text{ mag}/\text{arcsec}^2$ bedeutet einen 100-fach helleren Nachthimmel (Unihedron 2017). Sowohl Lichtintensität als auch Himmelshelligkeit wurden an den Beobachtungspunkten alle 15 min in ca. 1 m Höhe gemessen. Für die statistischen Analysen wurde dann jeweils der Mittelwert der drei Messungen verwendet. Auf Ebene der Landschaftsmatrix wurden Nachtlichtaufnahmen der Visible Infrared Imaging Radiometer Suite (VIIRS) an Bord des Suomi NPP (National Polar-Orbiting Partnership) Satelliten genutzt (Datenquelle: NOAA 2018, Datenstand: Januar 2013), um Lichtverschmutzung zu quantifizieren. VIIRS detektiert Licht im Wellenlängenbereich zwischen 500 und 900 nm in einer räumlichen Auflösung von 15×15 Bogensekunden-Rastern (NOAA 2018), was für den Raum Wien einer Rastergröße von ca. $380 \times 380 \text{ m}$ entspricht. VIIRS reagiert hoch sensibel auf geringste Mengen sichtbaren Lichtes (Liao et al. 2013; Miller et al. 2013). Das resultiert in Nachtlichtaufnahmen, die eine sehr gute Erfassung anthropogener Lichtquellen erlauben, weniger gesättigte Pixel in stark lichtverschmutzten Gebieten zeigen und damit eine bessere Darstellung stadinterner Charakteristika ermöglichen (Elvidge et al. 2013). Basierend auf diesen VIIRS-Nachtlichtaufnahmen wurde die mittlere

Helligkeit in einem Puffer von 250 m und 500 m um den jeweiligen Kartierungspunkt berechnet. Die Berechnungen wurden in ArcGIS 10.2 (ESRI) mit Hilfe des Werkzeuges Zonale Statistiken durchgeführt.

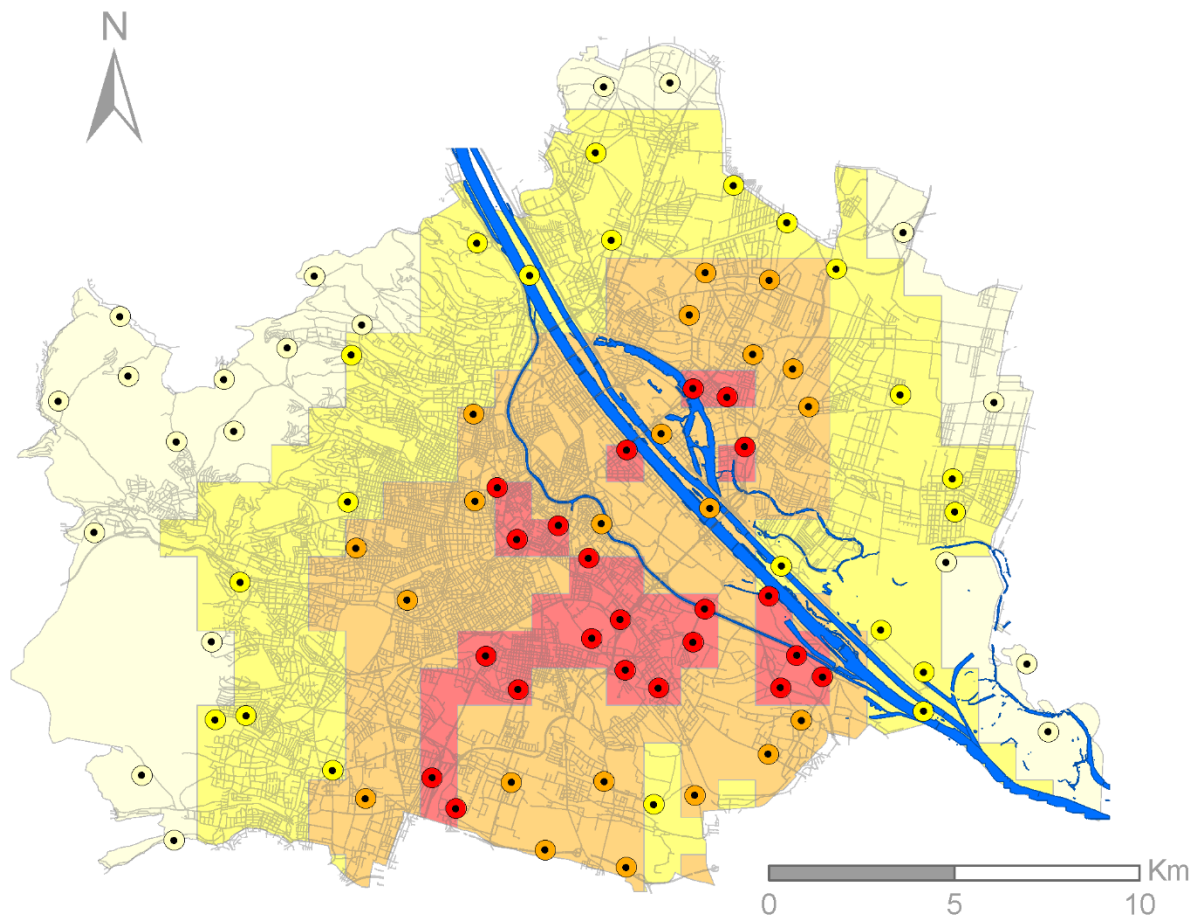


Abb. 1: Lage der 84 Zufallspunkte, an denen Vogelerhebungen durchgeführt wurden. Das Wiener Stadtgebiet wurde basierend auf VIIRS-Nachtlicht-Satellitenaufnahmen in vier Zonen unterteilt: hellgelb = kaum lichtverschmutzt ($< 5 \text{ nW}/(\text{cm}^2 \cdot \text{sr})$), gelb = leicht lichtverschmutzt ($5,01\text{-}15 \text{ nW}/(\text{cm}^2 \cdot \text{sr})$), orange = mäßig lichtverschmutzt ($15,01\text{-}25 \text{ nW}/(\text{cm}^2 \cdot \text{sr})$), rot = stark lichtverschmutzt ($> 25 \text{ nW}/(\text{cm}^2 \cdot \text{sr})$). Blaue Linien stellen den Verlauf der Donau und ihrer Nebengewässer dar, graue Linien das Straßennetz. – Overview on 84 random points, where bird surveys were carried out. The city of Vienna was divided into four zones based on VIIRS night time satellite images: bright yellow = hardly light polluted ($< 5 \text{ nW}/(\text{cm}^2 \cdot \text{sr})$), yellow = slightly light polluted ($5,01\text{-}15 \text{ nW}/(\text{cm}^2 \cdot \text{sr})$), orange = moderately light polluted ($15,01\text{-}25 \text{ nW}/(\text{cm}^2 \cdot \text{sr})$), red = strongly light polluted ($> 25 \text{ nW}/(\text{cm}^2 \cdot \text{sr})$). Blue lines indicate the river Danube and its backwaters, grey lines represent the road network.

Augengröße

Daten zur Augengröße (Mittelwerte) an den Untersuchungspunkten erfasster Vogelarten stammen aus unserer eigenen Datenbank (methodische Details zum Vermessen der Augendurchmesser siehe Schütz & Schulze 2014) oder von Thomas et al. (2002). Die Augengröße wurde für die statistischen Auswertungen in Relation zur Körpergröße gesetzt. Die daraus resultierende relative Augengröße entspricht dem Residuum der Regression zwischen log-transformierter absoluter Augengröße und log-transformiertem Körpergewicht. Daten zum Körpergewicht der einzelnen Vogelarten stammen aus Dunning (2008). Sofern vorhanden, wurden dabei Gewichtsangaben aus dem Winter verwendet. Nach Geschlecht getrennte Angaben zum Körpergewicht wurden gemittelt. Tab. 1 gibt einen detaillierten Überblick über die Daten zur Augengröße und zum Körpergewicht von 19 Vogelarten, die verwendet wurden, um deren relative Augengröße zu ermitteln.

Tab. 1: Datengrundlage, um die relative Augengröße einzelner Vogelarten zu ermitteln. Daten zum Augendurchmesser stammen von Thomas et al. (2002) oder unserer eigenen Datenbank. Daten zum Körpergewicht wurden Dunning (2008) entnommen. Die elf Vogelarten, die herangezogen wurden, um die Effekte von Lichtverschmutzung und relativer Augengröße auf den Aktivitätsbeginn zu ermitteln, sind fett gedruckt (AD = Augendurchmesser, SD = Standardabweichung, KG = Körpergewicht, N = Stichprobe, ED = Eigene Datenbank). – *Data used for calculating the relative eye size of bird species. Data on eye size derived from Thomas et al. (2002) or from our own database. Body mass data were extracted from Dunning (2008). The eleven species which were used to test for effects of light pollution level and relative eye size on the activity start of birds are printed in bold (AD = eye size diameter, SD = standard deviation, KG = body mass, N = sample size, ED = own database).*

Deutscher Artnamen	Wissenschaftlicher Artnamen	AD (mm)	SD	KG (g)	N	ED	Thomas et al. (2002)
Feldlerche	<i>Alauda arvensis</i>	4,77	0,06	40,85	3		X
Rotkehlchen	<i>Erithacus rubecula</i>	4,79	0,42	17,97	5	X	
Zaunkönig	<i>Troglodytes troglodytes</i>	3,41	0,25	8,74	22		X
Amsel	<i>Turdus merula</i>	7,07	0,48	83,35	3	X	
Singdrossel	<i>Turdus philomelos</i>	6,43	0,20	70	12		X
Schwanzmeise	<i>Aegithalos caudatus</i>	3,51	0,88	7,7	2	X	
Blaumeise	<i>Cyanistes caeruleus</i>	3,68	0,19	10,73	24	X	
Kohlmeise	<i>Parus major</i>	4,29	0,25	19,11	20	X	
Kleiber	<i>Sitta europaea</i>	4,5	0,12	23,1	2	X	
Waldbaumläufer	<i>Certhia familiaris</i>	3,6	0,14	8,5	2		X
Elster	<i>Pica pica</i>	6,63	0,11	206,1	2		X
Saatkrähe	<i>Corvus frugilegus</i>	8,57	0,32	485,7	3		X
Hausperling	<i>Passer domesticus</i>	4,01	0,10	30,4	2	X	
Feldperling	<i>Passer montanus</i>	4,05	0,26	23	127	X	
Buchfink	<i>Fringilla coelebs</i>	4,05	0,21	23,6	5	X	
Grünfink	<i>Chloris chloris</i>	4,07	0,26	30,65	8	X	
Stieglitz	<i>Carduelis carduelis</i>	3,74	0,11	15,8	9	X	
Gimpel	<i>Pyrrhula pyrrhula</i>	4,82	0,40	32,95	4	X	
Goldammer	<i>Emberiza citrinella</i>	4,7	0,26	29,8	10	X	

Statistische Analysen

Für die statistischen Analysen standen von 83 Kartierungspunkten Daten zur Vogelaktivität zur Verfügung, da an einem Punkt keine Vogelaktivität registriert werden konnte. An jedem Untersuchungspunkt wurde dabei pro Art nur jener Zeitpunkt berücksichtigt, an dem die jeweilige Art zum ersten Mal gehört und/oder gesehen wurde. Dieser Zeitpunkt wurde in Minuten nach (positive Werte) oder vor (negative Werte) Beginn der zivilen Dämmerung angegeben, um saisonalen Unterschieden in der Tageslänge gerecht zu werden. Es wurden nur jene Vogelarten berücksichtigt, die an mindestens vier Kartierungspunkten nachgewiesen werden konnten (Tab. 1). Aufgrund der Struktur unserer Daten berechneten wir lineare, gemischte Modelle mit Punkt-ID und Art als Zufallseffekte und relativer Augengröße, Lichtverschmutzung, minimaler Temperatur und Monat als Prädiktorvariablen. Im Zuge der Modellselektion wurden alle möglichen Kombinationen der unabhängigen Variablen miteinander verglichen und jene Modelle identifiziert, die das Informationskriterium minimieren. Hierfür wurden Modelle ihrem AIC (Akaike's Informationskriterium) folgend gereiht. Nur jene Modelle, die einen Unterschied < 2 hinsichtlich ihres AIC-Wertes zum besten Modell (= Modell mit dem kleinsten AIC-Wert) zeigten, wurden als bestgereimte Modelle bewertet (Richards et al. 2011; Symonds & Moussalli 2011).

Für jedes Modell wurde auch das Akaike-Gewicht berechnet, das die Wahrscheinlichkeit, mit der ein Modell die Zusammenhänge zwischen der Zielvariablen und den unabhängigen Variablen am besten vorhersagt, angibt. Die Modellselektion wurde getrennt für die vier Lichtverschmutzungsmaße Lichtintensität (Luxmeter), Himmelshelligkeit (Sky Quality Meter), VIIRS-Nachtlichtaufnahme 250 m und VIIRS-Nachtlichtaufnahme 500 m durchgeführt. Auch wenn der Aktivitätsstart zwischen Arten verglichen wurde, führten wir keine Tests hinsichtlich Signifikanz und Stärke eines phylogenetischen Signals durch, da unser Datensatz lediglich 11 Arten umfasste, die zudem aus sieben verschiedenen Familien (Alaudidae: eine Art, Muscicapidae: eine Art, Troglodytidae: eine Art, Turdidae: zwei Arten, Paridae: zwei Arten, Corvidae: eine Art, Fringillidae: drei Arten) stammten. Die statistischen Analysen wurden mit der Software R 3.4.3. (R Core Team 2014) durchgeführt, unter Verwendung der R-Pakete lme4 (Bates et al. 2015), MuMIn (Barton 2015) und visreg (Breheny & Burchett 2017).

Ergebnisse

Insgesamt wurde der Aktivitätsbeginn von 259 Vogelindividuen aus elf Arten analysiert. Vergleicht man die Zusammenstellung der bestgereihten Modelle getrennt nach den einzelnen Lichtverschmutzungsmaßen, ist die relative Augengröße in allen der bestgereihten Modelle enthalten (Tab. 2). Alle Lichtverschmutzungsmaße sind zwar in zumindest einem der bestgereihten Modelle enthalten, die VIIRS-Maße haben jedoch stärkeren Einfluss auf den Aktivitätsbeginn von Vögeln im Vergleich zur Lichtintensität (Luxmeter) und zur Himmelshelligkeit (Sky Quality Meter). Das VIIRS 250 m-Maß ist in allen bestgereihten Modellen und das VIIRS 500 m-Maß in drei der vier bestgereihten Modelle enthalten (Tab. 2). Zudem zeigt das Modell, das VIIRS 250 m, Monat und relative Augengröße als unabhängige Variablen enthält, den höchsten Wert hinsichtlich seines AIC-Gewichtes (Tab. 2). Größere Augen und ansteigende Lichtverschmutzung (basierend auf VIIRS-Nachtlichtaufnahmen) führen dabei zu einem früheren Aktivitätsbeginn (Abb. 2).

Tab. 2: Bestgereichte Modelle ($\Delta AIC < 2$) um den Aktivitätsbeginn von Vögeln im Wiener Stadtgebiet zu erklären, getrennt für die vier Lichtverschmutzungsmaße. Akaike's Informationskriterium (AIC), Unterschiede in den AIC-Werten einzelner Modelle zum bestgereichten Modell (ΔAIC), und Akaike-Gewichte (ω_i) sind für die jeweiligen Modelle aufgelistet. Unabhängige Variablen, die in allen bestgereichten Modellen für das jeweilige Lichtverschmutzungsmaß enthalten sind, sind fett und kursiv formatiert. – *Best ranked models ($\Delta AIC < 2$) explaining the activity start of birds in the city of Vienna, shown separately for each of the four light pollution measures. Akaike's Information Criterion (AIC), AIC-differences to the best ranked model (ΔAIC) as well as Akaike weights (ω_i) are listed for each of the models. Independent variables being included in each of the best ranked models for the respective light pollution measure are printed in bold and italic.*

a) Lichtintensität (Luxmeter)				
Modellnr.	Unabhängige Variablen	AIC	ΔAIC	ω_i
1	Min. Temperatur, <i>rel. Augengröße</i>	1862,3	0	0,23
2	<i>Rel. Augengröße</i>	1862,71	0,41	0,19
3	Monat, <i>rel. Augengröße</i>	1863,21	0,92	0,15
4	Lichtintensität, Min. Temperatur, <i>rel. Augengröße</i>	1863,44	1,14	0,13
b) Himmelshelligkeit (Sky Quality Meter)				
Modellnr.	Unabhängige Variablen	AIC	ΔAIC	ω_i
1	Min. Temperatur, <i>rel. Augengröße</i>	1862,3	0	0,24
2	<i>Rel. Augengröße</i>	1862,71	0,41	0,2
3	Monat, <i>rel. Augengröße</i>	1863,21	0,92	0,15
4	Himmelshelligkeit, Min. Temperatur, <i>rel. Augengröße</i>	1864,03	1,73	0,1
c) VIIRS 250 m				
Modellnr.	Unabhängige Variablen	AIC	ΔAIC	ω_i
1	<i>VIIRS 250 m, Monat, rel. Augengröße</i>	1858,5	0	0,42
d) VIIRS 500 m				
Modellnr.	Unabhängige Variablen	AIC	ΔAIC	ω_i
1	VIIRS 500 m, Monat, <i>rel. Augengröße</i>	1860,49	0	0,3
2	Min. Temperatur, <i>rel. Augengröße</i>	1862,3	1,81	0,12
3	VIIRS 500 m, Min. Temperatur, <i>rel. Augengröße</i>	1862,4	1,91	0,12
4	VIIRS 500 m, Min. Temperatur, Monat, <i>rel. Augengröße</i>	1862,45	1,97	0,11

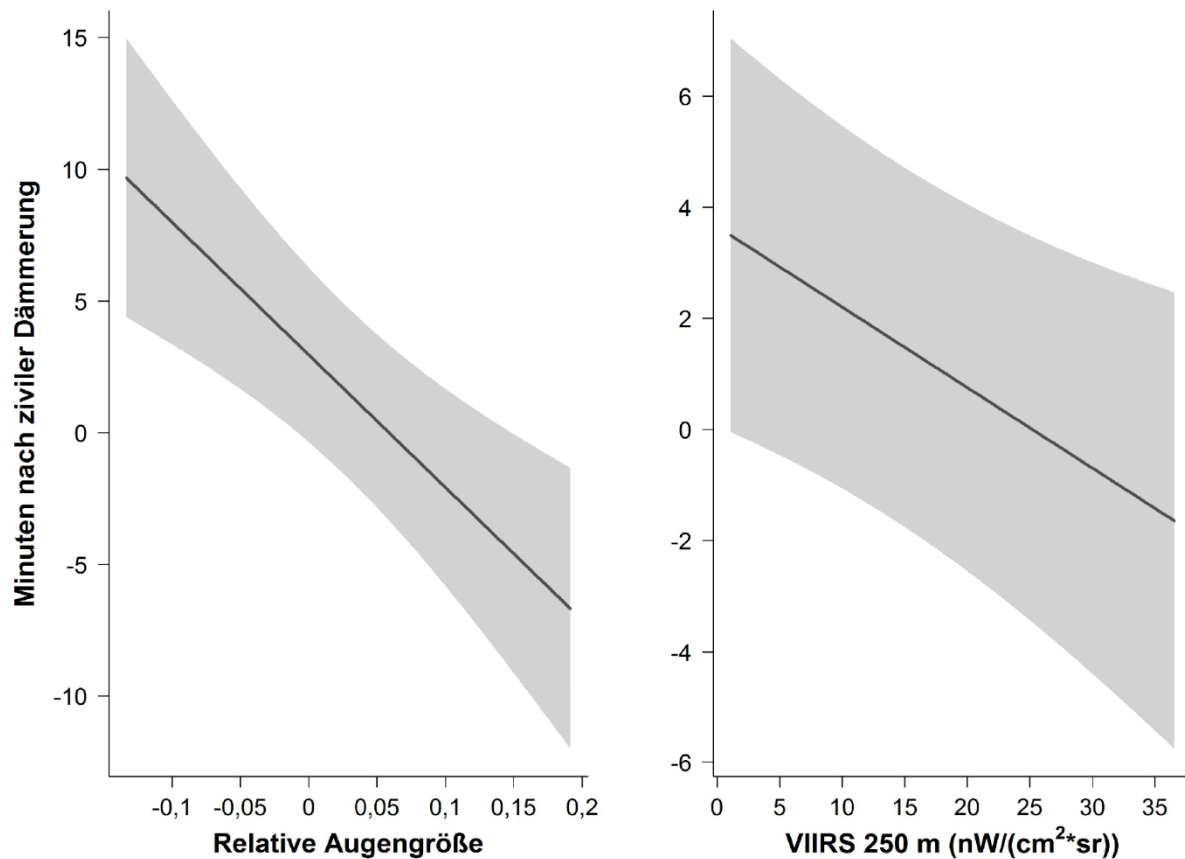


Abb. 2: Vorhergesagter Effekt der unabhängigen Variablen relative Augengröße und Lichtverschmutzung (basierend auf Satellitenaufnahmen) auf den Aktivitätsbeginn von Vögeln im Wiener Stadtgebiet. Vorhersagen basieren auf dem Modell in Tab. 2c, graue Bänder zeigen das 95 %-Konfidenzintervall an. – *Predicted effects of relative eye size and light pollution (based on night time satellite images) on the activity start of birds in the city of Vienna. Predictions are based on the model in Tab. 2c, grey ribbons indicate 95 % CI.*

Diskussion

Unsere multivariaten Analysen, die neben der Lichtverschmutzung gleichzeitig auch andere potentiell bedeutende Variablen wie Temperatur und Saison berücksichtigten, unterstreichen die Bedeutung der Augengröße als wesentlichen Einflussfaktor auf den Aktivitätsbeginn. Dabei sind Vogelarten mit größeren Augen in Relation zu ihrer Körpergröße früher aktiv als jene mit kleineren Augen (Thomas et al. 2002, 2004; Ockendon et al. 2009). Der Beginn der morgendlichen Aktivität wird also primär durch visuelle Fähigkeiten unter geringen Lichtintensitäten bestimmt (Thomas et al. 2004; Ockendon et al. 2009). Große Augen besitzen einen größeren Pupillendurchmesser und lassen mehr Licht in das Innere des Auges. Dadurch wird sowohl die optische Sensibilität (die Fähigkeit Licht von geringer Intensität wahrzunehmen) als auch die optische Auflösung (die Fähigkeit Details unter bestimmten Lichtbedingungen aufzulösen) erhöht – beides wichtige Eigenschaften für primär visuell gesteuerte Lebewesen wie Vögel (Thomas et al. 2004). Selbst unter schlechten Lichtbedingungen ist es dann möglich, Beute zu finden und effizient damit zu hantieren sowie sich annähernde Prädatoren rechtzeitig zu entdecken – Vorteile, von denen Vögel dank größerer Augen bei frühem Aktivitätsbeginn profitieren (Ockendon et al. 2009).

Neben der Augengröße hatte auch Lichtverschmutzung einen Effekt auf den Aktivitätsbeginn von Vögeln. Die Einflussstärke dieser Variable war in unserer Studie allerdings von ihrer räumlichen Auflösung abhängig. Kleinräumige Lichtverschmutzungsmaße, die von punktuellen Messungen mit Luxmeter und Sky Quality Meter stammen, hatten nur wenig Einfluss auf den Aktivitätsbeginn – ein Ergebnis das vereinzelt auch in anderen Studien zu finden ist (Da Silva et al. 2017, Welbers et al. 2017). Bei

Berücksichtigung der Lichtverschmutzung in einem größeren Puffer um die Beobachtungspunkte, zeigte sich aber sehr wohl eine Auswirkung auf den Aktivitätsbeginn von Vögeln. Wie bereits in anderen Studien gezeigt (Byrkjedal et al. 2012; Da Silva et al. 2014; Russ et al. 2015; Da Silva et al. 2017), führte dabei ein Anstieg der Lichtverschmutzung zu einem früheren Start der morgendlichen Aktivität. Neben Lichtverschmutzung und Augengröße wird der Aktivitätsbeginn bei Vögeln von einer Vielzahl weiterer interner (z. B. circadiane Rhythmen) und externer Faktoren (z. B. sozialen Interaktionen) beeinflusst. Experimente an Schwarzkopfmaisen *Poecile atricapillus* zeigten beispielsweise, dass der Beginn des Morgengesangs als Reaktion auf steigende Konkurrenz nach vorne verlegt und zudem auf das Verhalten von Reviernachbarn abgestimmt werden kann (Foote et al. 2011). Ein Vogel wird seinen Aktivitätsbeginn nach vorne verlegen, wenn sein Reviernachbar ein Territorium in einem stärker lichtverschmutzten Bereich innehat und dementsprechend früher am Morgen seine Gesangsaktivität startet, auch wenn punktuelle Messungen der Lichtverschmutzung sein eigenes Revier als wenig lichtverschmutzt ausweisen. Nachtlicht-Satellitenaufnahmen, die die Situation der Lichtverschmutzung auf einer größeren räumlichen Skala widerspiegeln, beschreiben damit nicht nur direkte sondern auch indirekte Effekte der Lichtverschmutzung und könnten daher besser geeignet sein, um den Einfluss von künstlichem Licht auf den Aktivitätsbeginn von Vogelarten zu beschreiben.

Zusammenfassend zeigen die Ergebnisse dieser Studie, dass v. a. Vogelarten mit großen Augen die morgendlichen Tagesrandzeiten stärker nutzen. Zudem führt ein Anstieg der Lichtverschmutzung zu einem früheren Aktivitätsbeginn. Die Ressourcennutzung entlang des Lichtgradienten könnte daher in lichtverschmutzten Gebieten zu Gunsten von Vogelarten mit größeren Augen verschoben werden, da diese Arten auf höhere Lichtverschmutzung stärker reagieren als andere (Kempenaers et al. 2010; Byrkjedal et al. 2012; Da Silva et al. 2017). Vogelarten mit größeren Augen könnten dann in lichtverschmutzten Gebieten von verlängerten Zeitfenstern für die Nahrungssuche oder vermehrten Kopulationen außerhalb des Paarbundes in höherem Ausmaß profitieren (Kempenaers et al. 2010; Byrkjedal et al. 2012; Da Silva et al. 2017). Kurzfristig führt das zu gesteigerten Überlebens- und Fortpflanzungsraten dieser Arten und damit zu möglichen Konkurrenzvorteilen. Langfristig könnte Lichtverschmutzung damit zur Homogenisierung von Vogelgemeinschaften beitragen (Da Silva et al. 2017). Davon dürften dann insbesondere Vogelgemeinschaften urbaner Habitate betroffen sein, da besonders das städtische Umfeld – das ohnehin schon mit den Folgen biotischer Homogenisierung zu kämpfen hat – stärker durch Lichtverschmutzung belastet ist als außerstädtische Lebensräume (McKinney 2006; Gil & Brumm 2014).

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2.6. Measuring the eye size of mist-netted birds: a comparison of two non-invasive methods

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Abstract

Relating eye size differences in birds to aspects of ecology and life history features offers interesting views on selective forces shaping eye size. However, data on eye size is hardly available. We compare two non-invasive methods for measuring the eye sizes of live birds: measures obtained using photos with a scale of the heads of mist-netted birds and published data based on measurements using a caliper. Both methods produced nearly identical data. Hence, we recommend using photos for measuring eye size instead of using a caliper, thereby – amongst other advantages – minimizing the risk of damaging the bird's eye.

Zusammenfassung

Unterschiedliche Augengrößen bei Vögeln in Beziehung zu ihrer Ökologie und Life history zu setzen, kann interessante Hinweise auf die für Augengröße verantwortlichen Selektionsdrücke liefern. Daten zu Augengrößen sind jedoch kaum verfügbar. Wir vergleichen zwei nicht-invasive Methoden, um die Augengrößen von lebenden Vögeln zu bestimmen: Messungen anhand skalierteter Porträtfotos von mit Japannetzen gefangenen Vögeln und publizierte Daten basierend auf Messungen mit einer Schublehre. Beide Methoden lieferten nahezu identische Werte. Daher empfehlen wir skalierte Fotos anstelle von Messungen mit einer Schublehre zur Bestimmung der Augengrößen, da dadurch – neben anderen Vorteilen – das Risiko einer Verletzung des Vogelauges minimiert wird.

Keywords

Eye diameter, portrait photographs, measurement method, non-invasive measurement

Own contribution

Study design: 50 %, data collection: 50 %, statistical analyses: 60 %, manuscript preparation: 100 %

Introduction

The amount of information captured visually by an animal depends on its eye size (Møller and Erritzoe 2010). Birds are characterised by particularly large eyes, which may be partly interpreted as an adaptation to rapid flight (Martin 1985). However, eye size is also determined by selection arising from required visual skills related to the communication with conspecifics, interactions with heterospecifics, foraging for food, and anti-predator behaviour (Møller and Erritzoe 2010). Relating eye size to different aspects of ecology and species' life history features will certainly offer more interesting views on selective forces shaping eye size. However, data on eye size is hardly available. To date several methods have been used to measure the eye size of birds: measuring the diameter and axial length of the eye using (1) fresh dead birds (Møller and Erritzoe 2010; Garamszegi et al. 2002) or (2) specimens preserved in ethanol after their eyes were fully inflated with injections of a preservative (Hall and Ross 2007); estimating the eye volume from skulls by using (3) spherical balls of Plasticine prepared by hand and then adjusted until they fitted into the eye socket of a fleshless skull (de Brooke et al. 1999) or by using (4) differently sized steel balls of known diameter (Thomas et al. 2004); (5) measuring the eye socket diameter from scale photographs of museum skulls (Thomas et al. 2004); and (6) measuring the diameter of the exposed eye surface of live birds using a caliper (Thomas et al. 2002, 2004). Although the eye shape is not necessarily spherical and can differ between diurnal and nocturnal birds (Hall and Ross 2007), measuring the maximum corneal diameter already appeared to be a reliable proxy for quantifying eye size (e.g. de Brooke et al. 1999). Measuring the diameter of the exposed eye surface of live birds with a caliper is a non-invasive measurement and, as such, has the advantage that the method can be applied without necessitating a bird's death. Furthermore, for many species, the access to fresh dead birds is extremely difficult (without killing them), or no skulls are accessible for measuring the eye socket.

However, the method of measuring the eye diameter of live birds by using calipers may bear the risk of damaging the eye. Therefore, we used portrait photographs of mist-netted birds with a scale overlay to measure their eye size. To evaluate the accuracy of this simple method, we compared our measurements with data published by Thomas et al. (2002) based on eye diameter measurements with a caliper using live birds. Furthermore, we tested the reliability of our measurements by using duplicate photographs and accounted for a potential recorder bias.

Methods

Eye size measurements



Fig. 1 Portrait photo of a Sedge Warbler *Acrocephalus schoenobaenus* with a scale on it used for measuring eye size. The measured diameter of exposed eye surface is indicated by a white line

Birds mist-netted at the Hohenau-Ringelsdorf ringing station (48°35'N, 16°55'E) – located in the Northeast of Austria – were used for eye size measurements. The 16 mist nets of the ringing station were set up in an area containing a mosaic of shallow water pools, semi-submerged vegetation, and muddy areas (Wichmann et al. 2004). Data on eye sizes of 32 bird species were collected during autumn migration on 23 days between August and October 2012 and in August 2013 (see Online Resource 1).

A portrait photo in lateral view with a scale overlay was taken for each bird at approximately the same level as the bird's eye. Therefore, the scale was fixed on the margin of a firm surface. Then, one researcher fixed the upper body of the bird between the thumb and index finger and subsequently positioned the head close to the scale to take the portrait photo (Fig. 1). By using the ruler tool option 'Use Measurement Scale' in Adobe Photoshop CS4 Extended (version 11.0.2), a custom measurement scale setting was created. Therefore, the pixel length of a 1 cm-unit of the ruler on the photo was defined. By using this custom scale setting, the maximal diameter of exposed eye surface (the distance between the medial and the lateral angle of the eye) was measured on every photo (Fig. 1).

Statistical analysis

In total, we measured the eye size of 656 birds belonging to 32 species (Online Resource 1). However, for analysis we only considered species of which at least two individuals were measured and for which eye size measurements were published by Thomas et al. (2002) (Online Resource 1). In total, 22 species remained for analysis. To test for the accuracy of our measurement method described above, we compared our eye size measurements with those of Thomas et al. (2002), who measured the exposed eye surface by using calipers.

For each of the 22 species, we calculated the mean eye diameter. These values were plotted against the measurements provided by Thomas et al. (2002). Additionally, the linear regression curve for the relationship between our data and the data of Thomas et al. (2002) and the angle bisector (indicating the position at which our values and the ones measured by Thomas et al. (2002) would be identical) are plotted. If our measurements would be identical to the eye size data published by Thomas et al. (2002), the resulting regression curve should completely overlay the angle bisector, and should have an intercept that does not deviate from zero and a slope that does not differ from one. Then, the coefficient of determination (r^2) should be 1. To test if eye size data of bird species differ between measurements obtained by using calipers (Thomas et al. 2002) and using photographs (own data), we calculated a paired t test. Finally, we tested the reliability of our measurements using duplicate photographs, which were available for a total of 81 birds belonging to 34 species. These photographs were of similar quality compared to the photographs initially used for measuring eye diameter. We also accounted for a potential recorder bias. For comparing our own data with the data of Thomas et al. (2002), eye diameter measurements were exclusively conducted by the first author, whereas measurements using the duplicate photographs were exclusively conducted by the second author. We again used a linear regression to estimate to what extent the measurements from both authors deviate.

Results

The linear regression curve describing the relationship between eye size values obtained by measuring the eye diameter of live birds with a caliper (Thomas et al. 2002) and using photographs of the birds' heads (own data), respectively, is nearly identical to the angle bisector, and all data points are located close to it (Fig. 2). This conclusion is further emphasized by a slope value of 1.05, an intercept of -0.19, and a very high coefficient of determination of $r^2 = 0.92$. This indicates nearly identical eye size measurements when comparing the two non-invasive methods. Furthermore, the values of both measurements did not differ significantly (paired t-test: $t = 0.61$, $df = 21$, $p = 0.547$).

Our method of quantifying eye size proved to be highly reliable (Online Resource 2). The calculated linear regression curve relating our first measurements done by the first author to measurements done by the second author using duplicate photographs had a slope value of 0.99, an intercept of 0.07, and a coefficient of determination of $r^2 = 0.91$.

Discussion

Our method of using photographs with a scale to measure birds' eye diameters proved to produce accurate measurements when compared with data on eye size diameters published before (Thomas et al. 2002). Hence, our method of eye size measuring does not lead to a directional bias through overestimating or underestimating eye size. Furthermore, repeated measurements of eye diameters by a second person using duplicate photographs demonstrate a high reliability of our method and a negligible recorder bias.

We see several advantages of this new method. First, using photographs with a scale instead of measuring eye diameter of live birds with a caliper is minimising the risk of damaging the bird's eye by touching the eye surface with the caliper because of uncontrolled movements of the bird. Secondly, taking portrait photos of the birds can reduce stressful handling time. Finally, once the photos are taken rechecking measurements is also possible. This increases reproducibility compared to caliper measurements, which potentially can be recorder-biased and lack the possibility of repeat measurements. Therefore, we strongly recommend this simple method for quantifying the eye size of birds trapped by mist-netting or other trapping methods.

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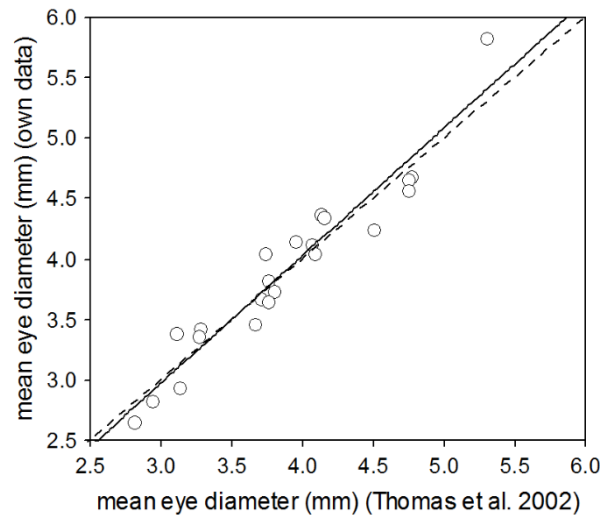
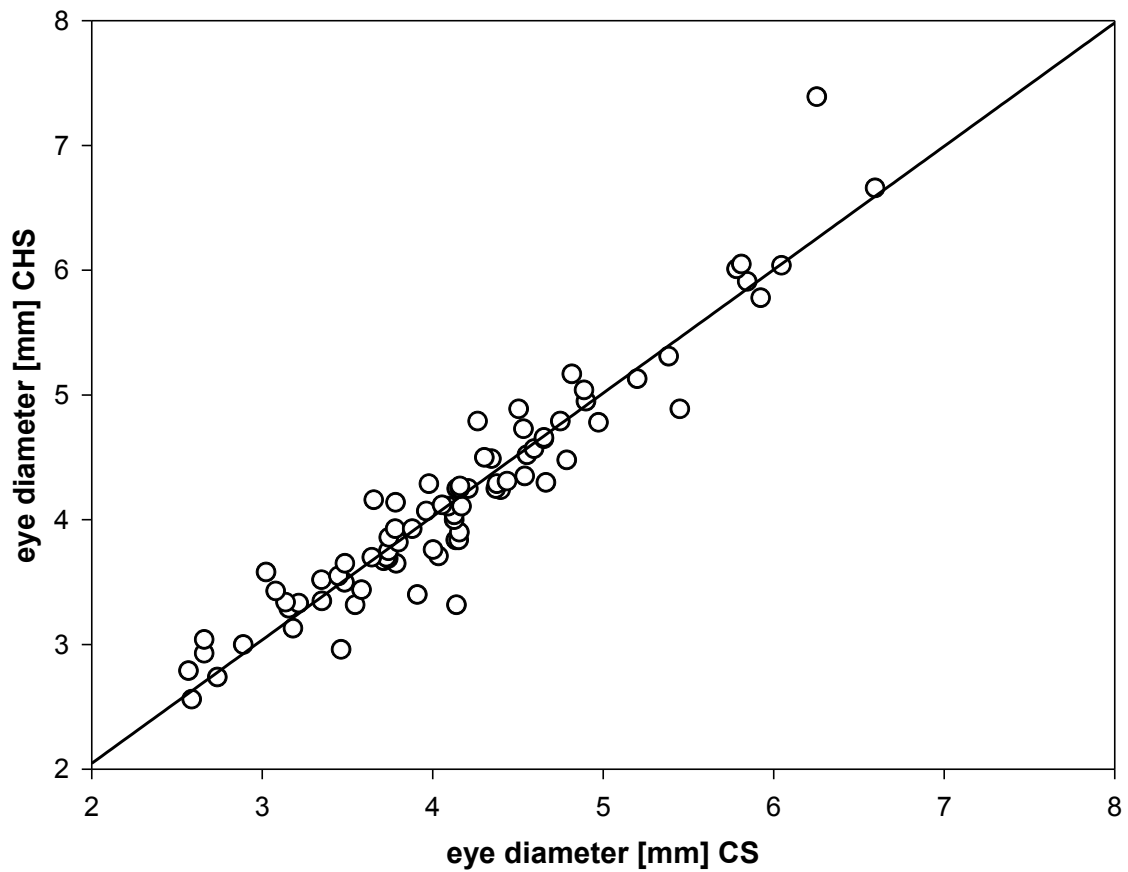


Fig. 2 Mean eye size (mm) of 22 passerine bird species based on own measurements using portrait photographs of bird heads with a scale plotted against measurements of Thomas et al. (2002), who measured eye diameter of live birds with a caliper. The relationship between both measurements is described by a linear regression curve (solid line); the angle bisector is indicated by a dashed line

Supplementary Material

Online Resource 1 Sample size (N), mean eye size measurements and standard deviation (SD) of 32 bird species trapped at the ringing station Hohenau-Ringelsdorf. The 22 bird species used for analysis are printed in bold.

Species	N	Mean eye size diameter [mm]	± SD
<i>Acrocephalus arundinaceus</i>	15	5.08	0.28
<i>Acrocephalus palustris</i>	77	3.88	0.30
<i>Acrocephalus schoenobaenus</i>	84	3.46	0.33
<i>Acrocephalus scirpaceus</i>	40	3.82	0.26
<i>Carduelis carduelis</i>	9	3.38	0.19
<i>Chloris chloris</i>	2	3.65	0.68
<i>Cyanistes caeruleus</i>	24	3.36	0.32
<i>Delichon urbica</i>	7	3.90	0.16
<i>Dendrocopos major</i>	2	6.13	0.44
<i>Emberiza citrinella</i>	11	4.35	0.43
<i>Emberiza schoeniclus</i>	29	3.74	0.32
<i>Erithacus rubecula</i>	4	4.68	0.40
<i>Gallinago gallinago</i>	3	6.69	0.28
<i>Hirundo rustica</i>	9	4.25	0.27
<i>Jynx torquilla</i>	7	4.54	0.22
<i>Lanius collurio</i>	23	5.83	0.54
<i>Locustella naevia</i>	3	3.67	0.12
<i>Luscinia megarhynchos</i>	3	4.66	0.32
<i>Luscinia svecica</i>	9	4.27	0.35
<i>Motacilla alba</i>	3	4.50	0.59
<i>Parus major</i>	20	4.05	0.26
<i>Passer montanus</i>	125	3.80	0.33
<i>Phylloscopus collybita</i>	46	2.82	0.33
<i>Phylloscopus trochilus</i>	22	2.94	0.22
<i>Prunella modularis</i>	36	4.12	0.24
<i>Saxicola torquata</i>	10	4.57	0.25
<i>Serinus serinus</i>	2	2.65	0.08
<i>Sylvia atricapilla</i>	7	4.14	0.22
<i>Sylvia borin</i>	4	4.37	0.34
<i>Sylvia communis</i>	16	4.05	0.57
<i>Sylvia curruca</i>	2	3.42	0.32
<i>Sylvia nisoria</i>	2	4.55	0.06



Online Resource 2 Linear regression curve for the relationship between eye diameter measurements done by the first author (CS) and measurements done by the second author (CHS) using duplicate photographs. N = 81 individuals belonging to 34 species.



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3. Synopsis

There is a growing body of research on the effects of urbanisation and its associated environmental changes such as noise pollution, light pollution and human disturbance on avian wildlife (Jokimäki et al. 2016, Vincze et al. 2016, Ciach & Fröhlich 2017 etc.). Thereby, studies focusing on city park bird communities of the temperate region are mainly settled during the breeding season (Suhonen & Jokimäki 1988, Jokimäki 1999, Fernández-Juricic 2004, Tryjanowski et al. 2017). Results of our studies will deepen the existing knowledge on the urban ecology of birds by paying particular attention to the situation during winter months. Effective management measures will then be facilitated to ensure suitable habitat conditions for wintering birds in urban environments. Especially birds from nearby rural areas – heavily struggling with depleted food resources and harsh weather conditions during winter (Ekman 1984, Macleod et al. 2005) – may then benefit from such management measures by increasingly dispersing to urban landscapes (Tryjanowski et al. 2015).

Most of our studies on the urban ecology of wintering birds rely on surveys being carried out in up to 36 city parks of Vienna, covering up to seven winters. To test for effects of light pollution on daily activity patterns of birds, considering species-specific differences of their visual capability, point counts were carried out between November 2014 and April 2015 at 84 randomly selected survey points within the city borders of Vienna.

Several studies have already identified park size as the key driver for maintaining a species-rich breeding bird fauna within the urban landscape (Nielsen et al. 2014, Huang et al. 2015). The results of our studies extend this prominent effect of park size to the non-breeding season. During winter an increase in park size promoted a higher taxonomical as well as functional diversity of bird communities. Large parks were also more likely occupied by forest specialists such as Great Spotted Woodpecker, Middle Spotted Woodpecker and Eurasian Sparrowhawk. Thereby, Sparrowhawk occurrence was not only positively affected by park size, but also by prey density and even more strongly by the interaction between these both variables. Our results also provided some evidence that city parks could act as refuges for birds during cold winters as the park occupancy of the Great Spotted Woodpecker increased significantly with decreasing mean winter temperatures. Besides local city park characteristics and weather conditions during winter, the composition of the urban matrix also affected bird diversity. Bird communities inhabiting city parks embedded in a highly urbanised landscape showed a loss of species richness and functional diversity.

Thereby, the urbanisation degree of the landscape was quantified as the proportion of sealed area in a given area around each city park. However, urbanisation not only causes transformations of land cover, turning natural habitats into built-up areas. Rather, urban ecosystems are characterized by complex interactions between social, economic and environmental variables (Alberti 2005). Hence, in another study we tested if night time satellite images can be used as a tool to integrate the large set of often correlated urbanisation metrics such as land use data or demographic measures into a single variable for assessing anthropogenic impact and its associated consequences on avian diversity. Results revealed that night lights deriving from satellite-based images can act as significant determinants for the permeability of the urban matrix and hence the avian diversity inhabiting remnants of semi-natural vegetation. Unlike other environmental or anthropogenic parameters used for quantifying urbanisation gradients, VIIRS night time images incorporate different facets of urbanisation into a single variable, drawing a much clearer picture of economic and demographic processes taking place within the borders of a city. This was also underlined by the results of our study. Models containing light pollution measures showed a better fit to our data than models containing the proportion of sealed area to quantify urbanisation degree.

Light pollution intensity quantified by night time satellite images also affected daily activity patterns of wintering birds, with higher intensities causing an earlier activity start. Small-scaled light pollution

metrics measured at census points didn't prove to have strong effects on the timing of daily activity. Further, the relative eye size of birds (eye size adjusted for differences in body size) was negatively related to the start of morning activity in birds during winter.

To summarise the results of our studies on the urban ecology of wintering birds in Vienna, park size is the main determinant for a species-rich and functional diverse avifauna within these urban green spaces. Thereby, the positive species-area relationship may partly be explained by higher habitat complexity and resource availability in large city parks (Nielsen et al. 2014). Furthermore, large city parks – as remnants of seminatural green space embedded in an urban landscape – have larger core areas that are unaffected by effects associated with habitat edges, such as a higher predation risk or higher levels of human disturbances (Fernández-Juricic 2001, Schneider et al. 2012). Hence, in large parks beside edge specialist species, being highly habituated to human activities and showing high breeding densities at urban park edges, also species with specific habitat requirements such as woodpeckers or birds of prey can be found in the more undisturbed core areas (Fernández-Juricic 2001). As in cities an enlargement of parks is difficult to realise, the implementation and maintenance of corridors such as alley trees along roads or scattered greenery could be a feasible alternative. This may not only enlarge the size of a city park, but may also increase the permeability of the urban landscape as the distances between green space remnants will be shortened (Fernández-Juricic 2000). As a consequence, dispersal abilities of habitat specialist species, reluctant to move through the unsuitable urban matrix, may increase. This in turn leads to higher chances of park occupation and positively affects the taxonomical and functional diversity of bird communities (Husté & Boulinier 2011).

Besides struggling with a shortage of suitable green space remnants urban birds also have to cope with a modified light regime. Thereby, the catastrophic effects of light pollution on night-migrating birds are already well known (Bairlein 2015, Van Doren et al. 2017). However, the more subtle influences of artificial night lighting on the community ecology of species are less recognized and pose a new focus in urban ecology research (Longcore & Rich 2004). Also the results of our study give some evidence that light pollution could contribute to shape urban bird communities. If naturally-early foragers, characterised by large eyes, benefit from a better exploitation of the night light niche compared to small-eyed species, they may gain higher winter survival rates. In the long run, this will intensify the already ongoing biotic homogenization within urban landscapes, underlining the pressing conservation challenge that light pollution poses to our modern world (Longcore & Rich 2004, Da Silva et al. 2017).

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4. Further publications and submitted manuscripts

2018

Literák I., R. Raab, S. Vyhnal, P. Spakovsky, H. Matušík & **C. Schütz** (submitted July 2018): Wintering grounds and summer vagrancy of young Red Kites from central Europe on a continental scale. *Ibis*.

Raab R., **C. Schütz**, M. Tiefenbach, P. Spakovsky, J. Steindl, N. Schönemann, S. G. Tarjányi & C. H. Schulze (submitted August 2018): Year-round spatial movements of Austrian Red Kites reveal rather individualistic than collective patterns. *Bird Study*.

Reckendorfer W., H. Badura & **C. Schütz** (resubmitted July 2018): Evaluating the effect of optimized reservoir management on sediment characteristics and grayling populations. *Ecology and Evolution*.

2017

Raab R., I. Literák, **C. Schütz**, P. Spakovszky, J. Steindl, N. Schönemann, S. G. Tarjányi, L. Peške, K. Makoň, J. Mráz, B. Maderič, V. Pečeňák, H. Matušík & C. H. Schulze: GPS-basierte Telemetriestudien an mitteleuropäischen Rotmilanen *Milvus milvus* – methodische Schwierigkeiten und analytische Möglichkeiten basierend auf ersten Ergebnissen. *Ornithologische Mitteilungen* 69: 245-260.

Ranner A., **C. Schütz** & F. Bauer: Zum Vorkommen ausgewählter gewässergebundener Vogelarten an der Leitha. *Vogelkundliche Nachrichten aus Ostösterreich* 28: 42-47.

2015

Raab R., **C. Schütz**, P. Spakovszky, E. Julius & C. H. Schulze: Optimizing the attractiveness of winter oilseed rape fields as foraging habitat for the West-Pannonian Great Bustard *Otis tarda* population during winter. *Bird Conservation International* 25: 366-376.

2013

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2010

Raab R., H.P. Kollar, H. Winkler, S. Faragó, P. Spakovszky, J. Chavko, B. Maderič, V. Škorpíková, E. Patak, H. Wurm, E. Julius, S. Raab & **C. Schütz** (2010): Die Bestandsentwicklung der westpannonischen Population der Großtrappe, *Otis tarda* Linnaeus 1758, von 1900 bis zum Winter 2008/2009. Egretta 51: 74-99.

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