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Contrasting effects of light and noise pollution interact with natural vegetation remnants: Human-related indicators of the habitat suitability for ungulates in the urban landscape

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ABSTRACT

The features of the urban landscape encouraging large ungulates expansion are not known. However, prevalence and abundance of wild boar *Sus scrofa* has been steadily increasing over the years, and nowadays the species has become a recognized component of urban wildlife in many parts of its range. The aim of this work was to select habitat and human-related factors that could affect the probability of the species occurrence and constitute the honest indicators of the habitat suitability for this ungulate in the urban landscape. The data on the presence of grubbed patches of ground (an honest indicator of occurrence) were collected on randomly selected sample plots (N = 100) within the city of Kraków (Poland). We found that wild boar used 45% of the sample plots. Whereas the occupied plots were spatially concentrated, the habitat variables increasing the probability of the species occurring in the urban landscape were the presence of large patches of woodland remnants and large areas of semi-natural meadows. However, the study also revealed a negative relationship between the presence of the species and artificial lighting but a positive one with anthropogenic noise pollution. Our results indicate that the urban landscape consists of surrogate habitats for this large mammal but light and noise pollution may have contrasting effects on the species' occurrence. This indicates that the influence of human-related factors on the attractiveness of natural vegetation remnants for wildlife is more complex than merely a limiting factor. This reveals high potential of light and noise pollution as indicators of the habitat suitability for ungulates in the urban landscape.

1. Introduction

Wild animals are frequently stimulated to develop a broad spectrum of responses to human-induced environmental changes (Tuomainen & Candolin 2011, Lowry et al. 2013). Small number of species such as mesopredator mammals, and ground-foraging, omnivorous or frugivorous birds can prosper in drastically different ecosystems such as urban ones (McKinney, 2006). Ungulates are large and diverse group of mammals, typically herbivorous, that use wide spectrum of habitats, including arid environments, grassland, wetland and woodland (Wilson & Mittermeier 2011). However, ungulates, being common game animals, usually avoid highly urbanized environments (Underwood & Kilheffer 2016; Loro et al. 2016), but marginal fractions of their populations are increasingly penetrating suburban areas (McCarthy et al. 1996; Kilpatrick & Spohr 2000; Mattila & Hadjigeorgiou 2015; Loro et al. 2016). The adaptation of ungulates to highly modified environments is a long-term process and their ability to colonize urban landscapes is a complex phenomena (Kilpatrick & Spohr 2000; Acevedo et al. 2005; Underwood & Kilheffer 2016). In some cases, colonization of urban landscape has been driven by population overabundance, and thereby food competition, in initially occupied natural environments (Warren 2011; Mattila & Hadjigeorgiou 2015).

The wild boar *Sus scrofa* inhabits a great variety of habitats (Heptner et al. 1988), from semi-deserts to swamps, forests and alpine meadows (Sjarmidi & Gerard 1988). An omnivorous animal, it has a broad feeding niche with a diet including roots, seeds, fruits, seeds, invertebrates and carrion. Foraging wild boar rely on olfactory cues to search for food by grubbing or rooting in the upper layers of soils (Briedemann 1990, Ballari and Barrios-García, 2014). The species is normally active at dusk and at night (Lemel et al. 2003; Keuling et al. 2008; Ohashi et al. 2013),

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but when not disturbed it can also be active during the daytime (Podgórski et al. 2013). These characteristics and their high intelligence (Marino & Colvin 2015) make wild boar ecologically extremely flexible and capable of adapting to highly-transformed environments such as farmlands and human settlements (Stillfried et al. 2017a, Stillfried et al. 2017b). During the last 20 years, wild boar numbers have increased greatly throughout its range of distribution (Wirthner et al. 2012). In consequence, ever greater numbers of these animals have been encroaching into human-dominated environments, including strongly urbanized ones like the interiors of large conurbations. The species has thus become acknowledged as a component of urban wildlife in many regions within its range.

Recent decades have witnessed the dynamic growth in abundance and expansion of wild boar into urban areas. Up to 2010, at least 44 cities in 15 countries, 8 of them in Europe (Belgium, France, Germany, Italy, Poland, Romania, Spain and the U.K.) reported having problems with wild boar (Cahill et al. 2012), and the number of cases still appears to be rising. Their colonization of urban areas is facilitated by environmental corridors, such as lines of trees along watercourses in built-up areas (Castillo-Contreras et al. 2018), and also wooded areas along transport corridors, principally railway lines. The easy availability of high-energy anthropogenic food further encourages wild boar to enter urban areas (Stillfried et al. 2017b). Indeed, there have been cases where people have deliberately left food for wild boar, given the increasing tolerance of their presence among human habitations (Conejero et al., 2019). Wild boar also enter towns and cities in search of new foraging areas (Castillo-Contreras et al. 2018), where flesh-fruit trees, planted purely for their aesthetic effect, are an attractive source of food, namely, the fruit that are lying on the ground beneath the trees. The higher temperatures in large towns and cities also make these places attractive to wild boar (Arnfield 2003), especially in winter, when the thinner snow cover presents a lesser obstacle to foraging (Mysterud et al. 1999; Ewald et al. 2014). A further factor encouraging wild boar to penetrate urban areas is that their main natural enemies – grey wolf *Canis lupus*, brown bear *Ursus arctos* and lynx *Lynx lynx* – are far less likely to hunt for them there (Tack 2018). Notable consequence of wild boar colonizing urban habitats is that their body mass becomes significantly greater than that of their woodland counterparts (Cahill et al. 2012).

To the colonization of urban areas, however, potentially attractive to wild boar, are attached a number of lethal and non-lethal risks to these animals. The most frequent such danger is posed by main roads, where the intensity of traffic and the speeds of moving vehicles often lead to collisions with wild animals (Zuberogoitia et al. 2014). Although culls are a major way of keeping wild boar populations down (Acevedo et al. 2006), the opportunities to shoot them in urban areas are limited for safety reasons, and often also because of the high level of empathy for animals among humans, who do not accept their killing as a means of reducing their numbers (Brown et al. 2000; Warren 2011; Tack 2018). Thus, as hoofed animals are rarely culled in urban areas, they have successfully been able to colonize some of them. The constant presence of people and their pets raises the level of stress among animals like wild boar living in towns and cities, heightening their vigilance and increasing the numbers and lengths of their movements, thereby compelling them to waste energy (Reimoser 2012; Padié et al. 2015). As flushed out wild boar tend to run away and hide in safe places (Thurfjell et al. 2013), patches of habitat in the landscape potentially offering shelter take on considerable significance.

Road infrastructure can be an obstacle to the free movement of animals among habitat patches, thus hindering food acquisition and limiting gene exchange (Forman & Alexander 1998; Hewison et al. 2009; Seidler et al. 2015). Traffic noise can disrupt the propagation of acoustic signals used by animals to communicate (Siemers & Schaub 2011; Mason et al. 2016). Animals which substantially rely on hearing tend to be over-vigilant in noisy environments (Klett-Mingo et al. 2016), which, in turn, increases energy expenditure and may lead to distress and exhaustion. Nonetheless, some animals are able to adapt to anthropogenic noise by adjusting their behavioural patterns: for example, birds adjust their escape strategies to the level of ambient noise (Petrelli et al. 2017) or alter their daily activity routines and use of space (Keuling et al. 2008; Ohashi et al. 2013; Johann et al. 2020).

Another factor which commonly limits the distribution of animals in urbanized landscapes is artificial lighting (Ciach & Fröhlich 2017). Such light disrupts navigation abilities in nocturnal animals (Longcore & Rich 2004; Beier 2006) and possibly their biological rhythms as well (Yeates 1949; Lincoln & Guinness 1972; Barber-Meyer 2007). By altering the natural light regime, artificial lighting may lead to shifts in reproductive activities (Robert et al. 2015) or discourage individuals from settling in lighted habitats (Azam et al. 2016). In consequence, the level of light pollution is negatively correlated with the occurrence of several groups of taxa (Azam et al. 2016; Ciach & Fröhlich 2017; Ciach & Fröhlich 2019). On the other hand, artificial lighting prolongs the photoperiod, which may be to the advantage of diurnal and crepuscular species, which can then remain active for a longer time (Erriksson et al. 1981; Dominoni & Partecke 2015). Such lighting can also lead to spatial and temporal disorientation and attraction of insects (Owens & Lewis 2018), affect the flowering, phenology and growth of plants (Bennie et al. 2016; Bennie et al. 2018), and thus cascade to further trophic levels, such as herbivores and their predators (Bennie et al. 2015; Ditmer et al. 2020).

Comparison of the diets of urban and rural wild boar populations shows that natural resources make up the staple diet, whereas anthropogenic food merely serves as a reserve source (Stillfried et al. 2017b). Differences in the behaviour of wild boar and their spatio-temporal utilization of habitats in areas variously affected by human pressure shows that these animals are capable of adapting their lifestyle to local conditions (Ohashi et al. 2013, Podgórski et al. 2013, Johann et al. 2020). This could be one of the factors explaining their recent rapid expansion in Europe. Urban wild boar also exhibit a greater tolerance towards the presence of humans (Stillfried et al. 2017a). Despite this, they are predominately active at night in urban areas so as to minimize contact with humans, in contrast to their natural habitats, where they may also be active during daylight (Podgórski et al. 2013). When active, moreover, the movements of these animals in urban areas tend to be more rapid than in their natural habitats (Podgórski et al. 2013).

The vast majority of studies of the wild boar's spatial ecology have been carried out in natural and semi-natural areas (Massei et al. 1997; Virgós 2002; Geisser and Reyer, 2004; Herrero et al. 2005; Fonseca 2008). Consequently, the reasons underlying the wild boar's highly successful colonization of urban areas, a mosaic of habitats variously modified by humans, have not been satisfactorily elucidated (Sütő et al. 2020). The aims of the present work were to (1) determine the prevalence of wild boar in an urban landscape and to (2) identify factors mediating the probability of the species occurring. We hypothesized that the main factor governing the presence of wild boar in cities would be the existence of patches of woodland and open habitats like arable fields and meadows, respectively offering shelter and foraging. At the same time, we presumed that human-related factors, i.e. light and noise pollution, would tend to discourage these animals from penetrating it. In the anticipated scenario, wild boar should prefer the remnants of forests and farmlands that are not influenced by human-related factors.

2. Methods

2.1. Study area

This study was carried out in the city of Kraków (S Poland, 50°05′ N, 19°55′ E). The city covers an area of 327 km^2 and has a population density of 2321 persons/km^2 (GUS, 2016). Urban greenery covers 47% of the city's overall area and is represented by gardens, squares, road verges, playgrounds, allotments and orchards, parks and cemeteries. Open areas cover 37% of the area and are represented by arable land (14%), spontaneous vegetation on fallow land (13%), meadows and pastures (8%), wetland vegetation (2%). Forests and woodland cover

11% of the area and are represented by natural and semi-natural scrub (5%), deciduous and mixed forest (4%), as well as damp, riparian forest and transformed tree stands (2%). Roads and railway lines make up 4% of the city's area (Dubiel & Szwagrzyk 2008). Built-up areas lie on an urbanization gradient – from the densely built-up city centre with limited green spaces, through the suburbs with a moderate number of buildings, located within different types of greenery, to the scattered buildings typical of a rural landscape and typically surrounded by patches of natural and semi-natural vegetation. The principal waterway in Kraków is the River Wisła (Vistula); six medium-sized tributaries and numerous smaller watercourses flow into the Wisła within the city limits (MIIP 2016) which, along with several small water bodies, cover 1% of the city's area. There is snow cover in Kraków for an average of 60–70 days and its mean thickness is 20 cm; however, both these parameters are exhibiting a long-term decrease, indicative of systematic climate warming (Falarz 1998). During the winter preceding the study period, the mean snow cover was 1.8 cm thick and it disappeared in mid-February.

2.2. Field methods

One hundred sample plots (1 km × 1 km squares) on which wild boar were to be surveyed (Fig. 1) were selected at random using Quantum GIS software (QGIS 2013) within the administrative borders of the city of Kraków. The distance between centroid of plots ranged from 1.00 km (adjacent plots) to 29.61 km (median = 9.00 km, quartile range = 5.83 – 13.00 km). The study was based on searching for grubbing sites (Fig. 2), because their presence is a reliable sign that wild boar have been utilizing an area. As grubbing is the wild boar's basic way of acquiring food between autumn, when ripening fruits and seeds are available on the ground or in the topsoil, and spring, when aboveground sources of food are not available (Sandom et al. 2013), sample plots were surveyed between 3 April and 26 May 2019. The timing of the field survey enable detection of the grubbing sites that has emerged between autumn 2018 and spring 2019. Because of the development of vegetation on the disturbed soil surfaces, grubbing sites become difficult to detect since late spring. Moreover, municipal services or private owners start to maintain urban greenery in late spring and restore sites damaged by the wild boars making them impossible to detect as season progress. In the light of the above, a study plot was treated as occupied if grubbed patches of ground were found on them – these are an honest sign of the species' presence and utilization of such a plot. However, this approach may tend to underestimate its actual distribution in the urban landscape. This is because when wild boar consume anthropogenic food (as a supplement to their natural diet), they do not leave visible, lasting signs of their presence. The tracks left by these animals in a given spot may merely indicate that they have been passing through, and are not proof that they constantly make use of that place. A further difficulty in using tracks as signs of the species' presence is that part of the area it moves around in is covered by a hard, impermeable surface (roads, pavements,

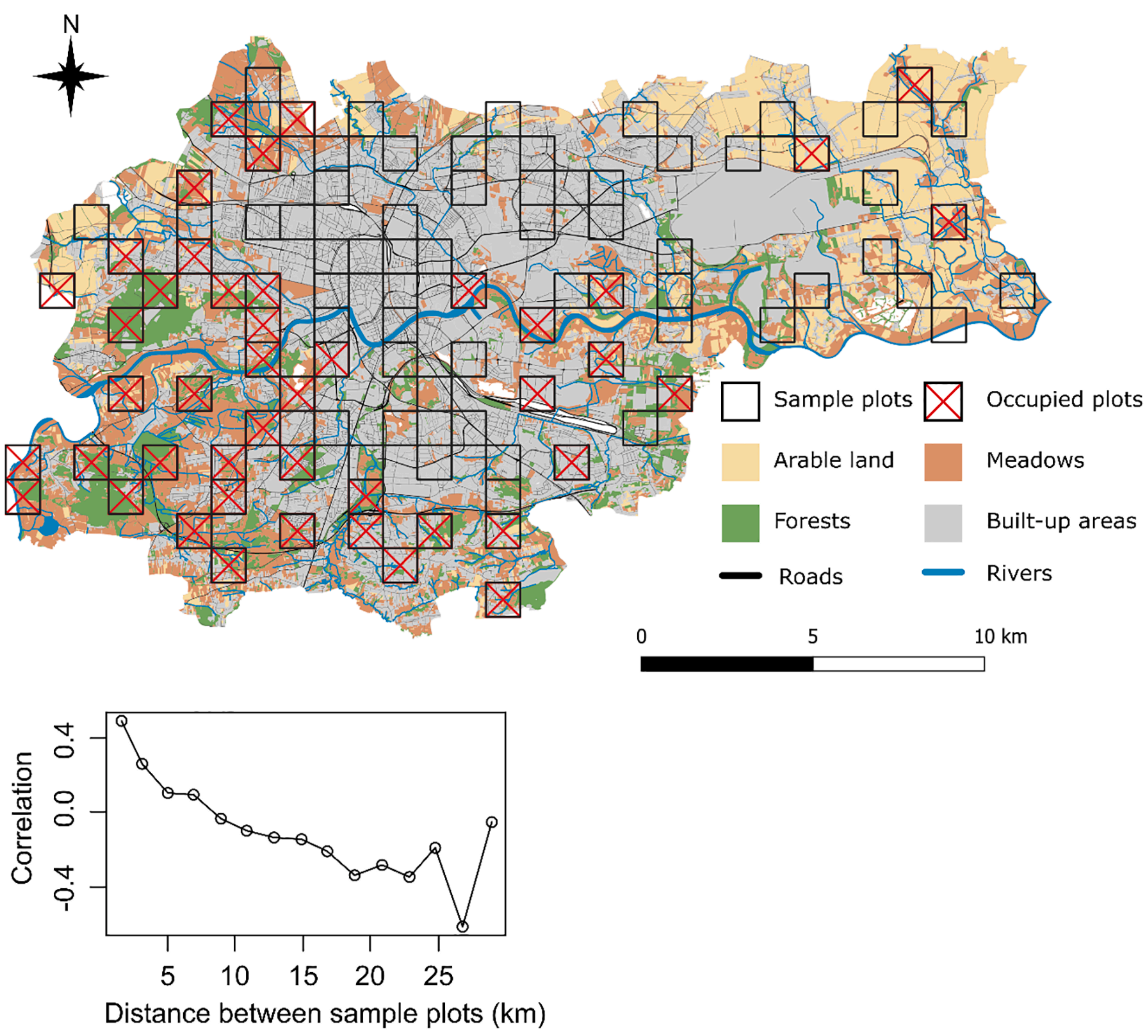

Fig. 1. Distribution of sample plots, distribution of plots occupied by wild boar *Sus scrofa*, and a correlogram showing the spatial correlation in the occurrence of this species within an urban environment (Kraków, S Poland).

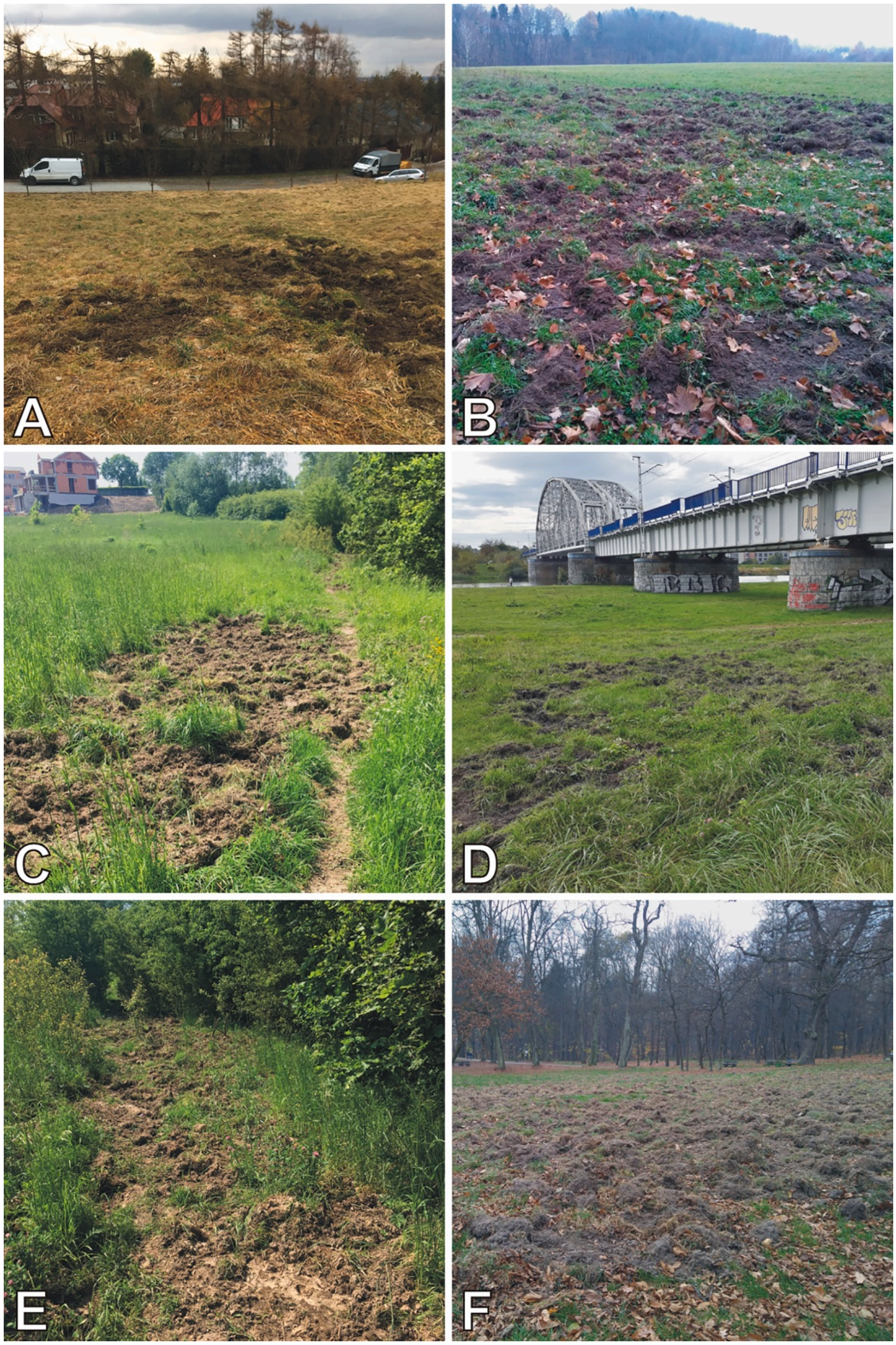

Fig. 2. Examples of grubbing (rooting) by wild boar *Sus scrofa* on grassy land (A); semi-natural meadow in a park (B), between low-density buildings (C) and in a river valley (D); forest edge (E) and forest interior (F) within an urban environment (Kraków, S Poland).

car parks), which in city centres makes it especially hard to detect the tracks left by animals passing through. Consequently, tracks recorded during the fieldwork were not treated as a sign of residence, as the inclusion of areas where wild boar were only temporarily present could have led to an overestimation of the species' permanent distribution.

A grubbed patch of ground was regarded as one where the foraging of wild boar had led to the soil being turned over and/or exposed, and such patches were considered separate if they were at least 100 m apart, or 50 m apart if there was an intervening obstacle such as a building or a fence. During the fieldwork, the route taken by the observer was recorded, as were the sites of grubbed patches. The mean distance covered by an observer on a study plot was 4266.8 m (±SD 1295.7; range 569.9–7347.7). The observer's mean speed of movement over the plot was ca 4 km/h, and the mean duration of such a plot survey was ca 1 h. During the fieldwork, all potential sites of the occurrence of wild boar were searched, i.e. urban greenery, woodland, parks and farmland. Not included were sites such as military areas, gated communities and gardens, to which access was impossible, usually to both observers and wild boar.

2.3. Environmental variables

The habitat parameters were defined on the basis of existing spatial database resources using GIS tools. Based on the atlas of the real vegetation of Kraków UMK (Urząd Miasta Krakowa) (2012), the effect of fieldwork done in 2006 (Dubiel & Szwagrzyk 2008), the total surface areas (ha) of forests, arable land and meadows on each sample plot were calculated. Natural meadows included pastures, uncultivated and fallow land, rock vegetation, swards, heaths and the communities of trampled areas. The area (ha) of the largest wooded habitat patch present in the vicinity of each sample plot was also calculated. Since wild boar are highly mobile animals, whose presence may be mediated by both the local and the wider landscape (presence of shelter and daytime resting places), the largest wooded patch was selected from all such patches within a radius of 1 km from the boundary of the study plot. The distance to a watercourse was calculated by measuring the distance from the central point of each sample plot to the nearest line of the layer of rivers located within the study area (WODGiK 2015).

Noise pollution was determined from the road noise emission database, compiled jointly by the Provincial Environmental Conservation Inspectorate in Kraków and the Kraków City Council in 2012 (MIIP 2016). The source data shows the noise level expressed in 9 classes of sound intensity (dB) (1 – <45, 2–45-50, 3 – 50.1–55, 4 – 55.1–60, 5 – 60.1–65, 6 – 65.1–70, 7 – 70.1–75, 8 – 75.1–80, 9 – > 80). Average noise levels at night (22:00 – 6:00) were used for these calculations. The noise level during the hours of darkness is highly correlated with that during the daytime ($r_S = 0.97$, $p < 0.001$) (Ciach & Fröhlich 2019). The mean noise class weighted by its range area was calculated for every sample plot. Since the data on noise emission were collected several years prior to the wild boar survey, a field test to assess potential between-year differences in noise level was performed, which indicated accuracy and permanency of the noise emission used in the analyses (Fröhlich & Ciach 2018).

Light pollution was determined on the basis of the Visible Infrared Imaging Radiometer Suite (VIIRS) supplied by The Earth Observations Group (EOG 2019). The raster layer contained the average radiance using night-time data from the VIIRS and was expressed in nanowatts per square centimetre per steradian ($nW/cm^2 \times SR$). The pixel size of the map was ~460 m (EOG 2019). The value of light pollution variable was calculated as the average of 100 points located in the regular grid covering each of sample plots. The raster layer was accessed on 15 June 2019 and contained data on light pollution in the period of sample plots surveys.

2.4. Data handling and analyses

The differences between studied environmental variables (Table 1) for plots on which the species was found and those where it was not found were analysed using Student's *t* test. The spatial correlation in the occurrence of wild boar was tested using Moran's I test, and the relationship between correlation coefficients and spatial distance was plotted. As we found evidence for spatial correlation in the occurrence of wild boar (see Results), we explained the species' occurrence using both basic Generalized Linear Models (GLM) and Generalized Linear Mixed Models accounting for spatial correlation (spatial GLMM; see Dormann et al. (2007)). The latter method allows the effect of environmental variables on the species' occurrence to be separated from the effect of its presence on adjacent plots. In both approaches, we used a binomial probability distribution with logit link function. The occurrence of the species was expressed by a dichotomous variable (0 – absent, 1 – present). In spatial GLMM, the distances between the sample plots in the form of a cross-diagonal distance matrix were included as a random term to which exponential decrease in spatial correlation was applied. Then, in both modelling approaches, we calculated candidate models including all the possible combinations of explanatory variables and compared them using the Akaike information criterion corrected for small sample sizes (AICc) (Supplementary materials, Table S1). Models with $\Delta AICc < 2$ were assumed to be those best describing the probability of wild boar occurring. To ensure that varying field effort among plots did not influence our results, the best models were checked for consistency with observer field effort as an additional explanatory variable. We performed deviance partitioning analysis for the variables that occurred in the top models. Assuming a set of all variables without fixed and random terms as the null model, we calculated the percentage of deviance explained by each variable alone (pure effects) and by all of their possible combinations (joint effects). To examine the consistency of results obtained with both modelling approaches, deviance partitioning analysis was performed separately for GLM and spatial GLMM. As sample plots were surveyed with a variable time effort, the distance (m) covered by the observer while monitoring the plot as recorded by the GPS receiver was used as an additional explanatory variable governing observer field effort. Prior to analyses, the autocorrelations between environmental variables were tested by Spearman's rank correlation test, which revealed no evidence of such a correlation, as this was $r_S < 0.5$ for every pair of variables. All the statistical procedures were carried out using R (R Development Core Team 2018) software, glmmTMB package (Brooks et al. 2017). The map presenting distribution of plots occupied by wild boar was prepared using Quantum GIS software QGIS (Quantum GIS Development Team) (2019) using the WSG 94 coordinate system.

3. Results

Wild boar were recorded on 45% of the randomly selected sample plots (N = 100). The occurrence of the species on the sample plots was spatially correlated (Moran's I = 0.11, $p < 0.001$) and was mainly concentrated in the suburbs (Fig. 1). Spatial correlation in the occurrence of wild boar decreased exponentially with lag distance, from $R^2 = 0.49$ in the case of adjacent plots to $R^2 = -0.05$ for the most distant plot pairs (Fig. 1). The environmental variables differentiating the surface areas occupied/non-occupied by wild boar were the surface area of forests, the surface area of meadows and the area of the largest wooded

Table 1
Descriptive statistics and results of Student's *t*-test for the environmental variables analysed on the study plots occupied/non-occupied by wild boar *Sus scrofa* in an urban environment (Kraków, S Poland; for a detailed description of the variables, see Methods).

Environmental variable	Description	Non-occupied		Occupied		t	p
		Mean	SD	Mean	SD		
Distance to the nearest river	Distance (m) between the centre of sample plot and the bank of the nearest watercourse.	502.6	450.9	274.3	278.2	2.96	0.004
Area of forests	Surface area (ha) of a given habitat type on a 1×1 km plot.	5.2	8.8	19.1	21.8	−4.31	0.000
Area of arable land		14.6	23.4	8.8	18.2	1.36	0.178
Area of meadows		12.9	13.7	30.4	19.9	−5.21	0.000
Light pollution	Mean night radiation of artificial lighting ($W/cm^2 \times sr$) on a 1×1 km plot.	29.5	19.6	15.7	11.0	4.23	0.000
Noise pollution	Mean class of night-time noise emission (dB) on a 1×1 km plot.	1.9	0.6	1.8	0.7	0.67	0.502
Area of the largest wooded patch	The area (ha) of the largest wooded patch present within a radius of 1 km from the boundary of the plot.	394.7	735.3	2124.0	2085.5	−5.73	0.000

patch, which were larger on occupied than non-occupied plots (Table 1). Moreover, the distance to the nearest river and night-time artificial light pollution were smaller on occupied plots than non-occupied ones (Table 1).

The GLMs (Table 2) showed that the probability of wild boar occurring was correlated positively with the magnitude of the woodland patch present within 1 km of the study plot (Models 1, 2, 3), the surface area of meadows (Models 1, 2, 3), the surface area of forests (Model 3) and the level of noise (Models 1, 2, 3), but negatively with the surface area of arable land (Models 1, 2, 3), the level of night-time artificial light pollution (Models 1, 2, 3) and the distance to the nearest river (Model 2).

The spatial GLMMs (Table 3) indicated that the probability of wild boar occurring was correlated positively with the magnitude of the largest woodland patch present within 1 km of the study plot (Models 1, 4), the surface area of meadows (Models 1, 2, 3, 4) and the level of noise (Models 1, 2, 3, 4), but negatively with the surface area of arable land (Models 3, 4) and the level of night-time artificial light pollution (Models 1, 2, 3, 4). The models incorporating observer field effort as an additional explanatory variable did not alter the results of either modelling approach (Supplementary materials, Tables S2 and S3).

Spatial randomness explained 23.0% of the variance, the value of which was higher than any other environmental variable alone (Table 4). The set of variables included in the best models obtained with GLM and spatial GLMM overlapped, yet each method returned different results with regard to the deviance explained by a given environmental variable. In spatial GLMM, night-time artificial light pollution was the single variable (pure effect) with the highest percentage of deviance explained, followed by the surface area of meadows and the area of the largest wooded patch. In GLM, the single variable (pure effect) with the highest percentage of deviance explained was the area of the largest wooded patch, followed by the surface area of meadows and night-time artificial light pollution. Both modelling methods showed that the surface area of arable land and noise pollution had low though significant explanatory power for the probability of the species occurring (Table 4). The combination of all variables explained 41.3% and 43.2% of the deviance in the dataset in GLM and spatial GLMM, respectively (Table 4).

Table 2
Generalized Linear Models (ΔAICc < 2) explaining the probability of wild boar *Sus scrofa* occurring in an urban environment (Kraków, S Poland); for a description of the variables, see Methods and Table 1; for the models including observer field effort, see Table S2 in the Supplementary Materials).

Variable	Estimate	SE	z	Pr(>|z|)
Model 1, AICc = 93.7				
Intercept	−0.28	0.31	−0.90	0.370
Area of arable land	−1.02	0.45	−2.28	0.022
Area of the largest wooded patch	0.93	0.43	2.15	0.032
Light pollution	−1.74	0.58	−2.98	0.003
Area of meadows	0.87	0.34	2.58	0.010
Noise pollution	0.69	0.30	2.27	0.023
Model 2, AICc = 95.1				
Intercept	−0.34	0.32	−1.05	0.291
Area of arable land	−1.03	0.45	−2.27	0.023
Area of the largest wooded patch	0.95	0.43	2.20	0.028
Light pollution	−1.65	0.59	−2.81	0.005
Area of meadows	0.78	0.35	2.23	0.026
Noise pollution	0.67	0.31	2.19	0.028
Distance to the nearest river	−0.38	0.41	−0.91	0.364
Model 3, AICc = 95.4				
Intercept	−0.25	0.31	−0.81	0.416
Area of arable land	−0.86	0.48	−1.78	0.076
Area of forests	0.33	0.46	0.73	0.467
Area of the largest wooded patch	0.86	0.43	2.03	0.042
Light pollution	−1.56	0.63	−2.49	0.013
Area of meadows	0.90	0.34	2.61	0.009
Noise pollution	0.67	0.31	2.19	0.029

Table 3
Generalized Linear Mixed Models accounting for the spatial correlation (ΔAICc < 2) explaining the probability of wild boar *Sus scrofa* occurring in an urban environment (Kraków, S Poland); for a description of the variables, see Methods and Table 1; for the models including observer field effort, see Table S3 in the Supplementary Materials).

Variable	Estimate	SE	z	Pr(>|z|)
Model 1, AICc = 94.9				
Intercept	−0.83	1.52	−0.55	0.584
Area of the largest wooded patch	1.00	0.65	1.52	0.128
Light pollution	−2.05	1.03	−1.99	0.047
Area of meadows	1.35	0.60	2.27	0.023
Noise pollution	0.89	0.46	1.95	0.051
Model 2, AICc = 95.0				
Intercept	−1.43	2.35	−0.61	0.542
Light pollution	−2.68	1.25	−2.14	0.032
Area of meadows	1.52	0.75	2.04	0.041
Noise pollution	0.95	0.53	1.80	0.072
Model 3, AICc = 95.2				
Intercept	−0.94	1.53	−0.62	0.537
Area of arable land	−0.95	0.66	−1.44	0.149
Light pollution	−3.00	1.19	−2.51	0.012
Area of meadows	1.25	0.64	1.96	0.050
Noise pollution	0.94	0.48	1.95	0.051
Model 4, AICc = 95.8				
Intercept	−0.60	1.01	−0.59	0.553
Area of arable land	−0.78	0.64	−1.21	0.225
Area of the largest wooded patch	0.84	0.64	1.30	0.192
Light pollution	−2.38	1.08	−2.19	0.028
Area of meadows	1.16	0.57	2.04	0.041
Noise pollution	0.87	0.44	1.96	0.050

4. Discussion

We found patches of ground grubbed up by wild boar on nearly half of the randomly selected study plots in Kraków and that they were especially concentrated on the city's outskirts. This shows that wild boar commonly utilize moderately urbanized areas for foraging, mainly in the suburbs, but also quite close to the city centre, albeit to a lesser extent in the latter (Fig. 1). Our results show unequivocally that whether or not we take the spatial correlation into consideration, the high probability of these animals occurring in an urban area is determined by the availability of extensive meadows and large patches of woodland. The study also revealed the significant negative influence of night-time artificial lighting on the species' presence within the city. However, we also found a weak though significantly positive relationship between the occurrence of wild boar and the level of anthropogenic noise. The response of these animals to urbanization is therefore more complex: they respond negatively to light pollution but do not appear to avoid noisy areas.

Earthworms, insects, snails and small vertebrates, present in open habitats, are important components of the wild boar's diet (Tack 2018). Natural open areas within a conurbation, including fallow land, meadows and pastures, especially if they lie adjacent to woodland complexes, are potential foraging areas for wild boar. The various ways in which open areas are managed by humans, where patches of mown and tall, unmown vegetation adjoin each other, enable foraging animals to remain concealed. In the city of Kraków, open areas usually border on woodlands or copses, forming a spatial mosaic of habitats where wild animals can quickly find shelter in case of danger. We noted that wild boar for preference foraged in extensively managed areas, that is to say, semi-natural meadows supporting tall grasses, reeds *Phragmites australis*, or patches of non-native goldenrods *Solidago* spp. offering shelter around the margins of such land. However, our research showed that

Table 4
Deviance partitioning analysis for the probability of wild boar *Sus scrofa* occurring in an urban environment (Kraków, S Poland). The values show the percentage of deviance explained by single variables (pure effects) and combinations of variables (joint effects), for both Generalized Linear Models (GLM) and Generalized Linear Mixed Models accounting for spatial correlation (spatial GLMM). The values with the highest percentage of deviance explained are highlighted in bold.

	Combinations of variables	GLM	spatial GLMM
	Spatial randomness only	-	23.0
Pure effects	Area of arable land (arable land)	1.4	23.2
	Area of meadows (meadows)	17.2	30.7
	Area of the largest wooded patch (wooded patch)	**22.2**	28.0
	Light pollution (light)	12.5	**31.6**
	Noise pollution (noise)	0.3	23.2
Joint effects, two variables	meadows + noise	17.7	36.1
	light + noise	14.4	33.6
	light + meadows	21.8	**36.7**
	wooded patch + noise	22.2	28.3
	wooded patch + meadows	**31.9**	34.9
	wooded patch + light	26.8	33.5
	arable land + noise	2.2	23.4
	arable land + meadows	18.6	30.7
	arable land + light	27.8	34.4
	arable land + wooded patch	22.3	28.0
Joint effects, three variables	light + meadows + noise	25.1	**40.3**
	wooded patch + meadows + noise	33.2	36.2
	wooded patch + light + noise	29.1	35.5
	wooded patch + light + meadows	33.4	38.4
	arable land + meadows + noise	18.8	34.5
	arable land + light + noise	30.9	37.1
	arable land + light + meadows	31.6	37.9
	arable land + wooded patch + noise	22.3	28.3
	arable land + wooded patch + meadows	32.3	34.9
	arable land + wooded patch + light	**33.6**	35.8
Joint effects, four variables	wooded patch + light + meadows + noise	37.0	**42.1**
	arable land + light + meadows + noise	36.1	41.9
	arable land + wooded patch + meadows + noise	33.3	36.2
	arable land + wooded patch + light + noise	36.1	38.4
	arable land + wooded patch + light + meadows	**37.4**	39.3
Total	arable land + wooded patch + light + meadows + noise	**41.3**	**43.2**

those parts of the city with a large proportion of arable land were not occupied by wild boar. Farmland, mainly where maize, potatoes and cereals are grown, constitutes a key source of food for wild boar during the growing season (Schley & Roper 2003, Thurfjell et al. 2009). This result was due to the fact that we carried out our fieldwork in spring, when the possibilities of detecting the animals on arable land, where they feed on aboveground biomass, were limited. In spring, little food is available on arable land, whereas ungulates encroach on to such land mainly in late summer and early autumn, until the crops have been harvested (Morelle & Lejeune 2015). Furthermore, farmland has little to offer in the way of underground food (mostly beetle larvae), so wild boar seldom grub around on it (Schley et al. 2008). Again, the consumption of aboveground plant parts or anthropogenic food does not leave behind visible traces such as grubbed patches. Thus, wild boar may be more widely distributed in the urban areas of Kraków than we were able to establish, since in the summer and autumn they may also be present on land where crops are growing. The spatial and temporal differentiation of food availability for wild boar is known to trigger its migrations among patches of different habitats from season to season (Sütő et al. 2020).

Woodlands are the main habitat offering shelter and daytime resting places to wild boar (Abaigar et al. 1994; Podgórski et al. 2013). Although woodlands within urban areas are not usually very large, they are not managed for timber production, and their penetration by humans, apart from certain designated areas, is not usually intensive. Some of these urban woodlands have no tourist infrastructure at all apart from paths for walkers and cyclists: these channel the movement of people, so that few venture into the adjacent woods. In addition, the local inhabitants may deliberately avoid places known to harbour wild boar for fear of being attacked by these animals (Kotulski & König 2008) and of diseases and parasites they may carry, especially ticks (Mora et al. 2012; Di Luca et al. 2013; Duscher et al. 2015; Fernández-Aguilar et al.

2018). Finally, people are generally unwilling to enter so-called neglected areas, which may be muddy and overgrown. The closeness of a woodland, offering shelter and resting places, is the key aspect of foraging areas selected by wild boar (Thurfjell et al. 2009). Moreover, woodland complexes also are a food resource, where there are fruiting trees, woodland invertebrates, the roots and tubers of plants, not to mention carrion (Meriggi & Sacchi 2001). Thus, even a fairly small patch of urban woodland can act as a daytime refuge and convenient foraging area for wild boar.

One of the factors mediating the occurrence of wild boar in urban areas is the presence of areas with natural access to water for drinking and bathing (Marsan & Mattioli 2013). In addition, watercourses act as migration corridors (Romanowski 2007; Rodriguez-Iturbe et al., 2009), and rivers maintained in a natural state enable large mammals to colonize towns and cities (Ciach & Fröhlich 2019). Watercourses and their associated clumps of trees and patches of alluvial woodland often provide shelter for wild boar, as well as drinking pools and wallow sites. We found that the areas inhabited by wild boar did indeed lie close to watercourses, although this variable was not of key importance in explaining the probability of its occurrence. This result can be partially put down to the presence of buildings or road infrastructure close to river banks or the local removal of riparian trees, which reduces the patency of potential environmental corridors.

By affecting physiological processes and behaviour, artificial lighting can mediate the occurrence and density of animals in a given area (Azam et al. 2016; Andersson et al. 1998; Ciach & Fröhlich 2017; Froidevaux et al. 2017). As ungulates are predominantly active at night in urban areas, they are almost always within range of artificial lighting (Hewison et al. 2009; Pagon et al. 2013). However, the effect of artificial light on wild boar populations inhabiting natural areas is not known: these animals rely mainly on their relatively well-developed senses of smell and hearing, using sight to a lesser extent (Conley et al. 1972; Eisenberg & Lockhart 1972; Nummela et al. 2013). Nonetheless, experimental manipulation of the photoperiod can elicit significant reactions in this species (Andersson et al. 1998). Avoidance of brightly lit parts of a town may be another temporal segregation strategy besides nocturnal activity which, together with spatial segregation strategies, helps to reduce contacts with humans to a minimum. Artificial lighting may also be a component of the "urban landscape of fear", associated as it is with the greater activity of people (walkers, cyclists) in places well illuminated at night. The avoidance of foraging in places that an animal associates with the presence of humans has been demonstrated in a study of bears (Lodberg-Holm et al. 2019). Even nonlethal human activities and the presence of human infrastructure are perceived by mammals as a risk and induce shifts in behaviour (Gaynor et al. 2018).

The results of this study do not indicate that noise adversely affects the probability of wild boar occurring in the city; to our surprise, noise pollution had a positive, though weak, effect on its occurrence. The main source of noise in urban Kraków is road traffic (MIIP 2016). As disturbance by road vehicles is common and highly predictable, urban wild boar ignore it and can be found quite close to roads (Thurfjell et al. 2015; Stillfried et al. 2017a). Enhanced tolerance towards moving vehicles and the noise they generate is common among ungulates (Stankowitch 2008). This is probably because these animals become habituated to noise, that is, they gradually become accustomed to a repeated stimulus (Cahill et al. 2012), in this case, noise. Domesticated wild boars are regarded as cognitively complex animals (Marino & Colvin 2015), capable of navigation (by smell) and orientation (spatial memory). As a result, they can develop complex movement strategies in order to cope with extraneous factors (Morelle et al. 2015), such as remaining indifferent to road traffic and the noise it produces. At the same time, high noise levels in some habitats may discourage people from visiting them. This applies in particular to woodlands and meadows, which are potential areas for human recreation; if such places are extremely noisy, people will be far less likely to visit them, as the expected conditions for recreation will not be met. Hence, the absence of people (and their dogs) moving around them will minimize direct disturbance of the animals there.

It should be stressed that encroachment of ungulates into the urban landscape could be a more complex process than that revealed by our coarse-type habitat models. Easily accessible areas of managed urban greenery and their spatial arrangement, like allotments, gardens, cemeteries, roadside verges, parks and squares, are potential sources of food for wild boar, albeit becoming the less accessible, the closer they are to the city centre (Sütő et al. 2020). The restricted access to such areas may be due to the density of buildings, as well as walls and fences, and on private property, dogs can scare off wild animals. The attractiveness of managed urban greenery to wild boar must therefore be limited. In addition, wild boar grubbing causes damage to managed urban green areas, which in turn leads to conflicts with owners or the users of urban public space (Kotulski & König 2008). In consequence, these mounting conflict situations may lead to further areas of managed greenery being fenced off, or to single individuals being scared off, captured or even shot. In some parts of the world, the damage caused by ungulates in urban areas has led to selected areas being closed off (Boone & Hobbs 2004; Harrington and Conover, 2006), and to steps being taken to reduce their populations (Brown et al. 2000; Warren 2011). In spite of the restrictions on hunting because of the proximity of buildings and the presence of humans, in recent years some 200 wild boar have been culled annually in the Kraków conurbation (Szyjka & Wajdzik 2017). However, there is one aspect preventing the accurate assessment of the degree to which wild boar make use of managed urban greenery: the damage caused by the animals is usually rapidly made good in that the grubbed patches of soil are raked over and resown by the owners or administrators of the land so affected.

The increasing ubiquity of wild boar, in combination with ever-expanding urbanization, that is, humans encroaching on to terrain previously occupied by these animals, is a source of conflict between them and people (Massei et al. 2011; Barrios-Garcia & Ballari 2012). The foraging of wild boar on managed areas causes damage in parks and on roadside verges, in sports stadia and backyards, that is costly to repair and reduces their aesthetic value, and this generates negative attitudes among people towards these animals. Indeed, wild boar are potentially dangerous animals, and injuries to people as a result of vehicle collisions with them (Kotulski & König 2008) as well as cases where they have actually attacked people, make urban dwellers very wary of them (Chauhan et al. 2009). Finally, wild boar are potential carriers of diseases and parasites, such as African Swine Fever (ASF) (Blome et al. 2013), which will inevitably lead to people demanding that wild boar populations be kept in check.

5. Conclusions

A species of considerable ecological and behavioural plasticity, the wild boar has successfully colonized radically transformed ecosystems like towns and cities, where it has achieved a high prevalence. When choosing its habitats, this species seeks above all food and shelter; under natural conditions it finds these in open terrain and woodlands, respectively. At the same time, the distribution of the wild boar in urban areas is significantly mediated by human-related factors. Key to its spatial distribution in urban ecosystems is the avoidance of places lit up at night. This may be a strategy to prevent direct contact with humans, who tend to congregate in such artificially lighted areas at night. The wild boar's preference for spots with high noise levels is a reflection of its very considerable cognitive and adaptive powers: it is very likely capable of accurately assessing danger and of ignoring predictable and harmless stimuli like moving vehicles on roads and to utilize patches of habitat where noise levels are high, as they will probably be free of people.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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