Current Zoology, 2018, 64(5), 575–583
doi: 10.1093/cz/zox061
Advance Access Publication Date: 31 October 2017
Article

Article

Noise shapes the distribution pattern of an acoustic predator

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Received on 8 July 2017; accepted on 14 September 2017

Abstract

Noise, an obvious effect of urbanization, has a negative impact on animal vocalizations and the hunting efficiency of acoustic predators. However, the influence of noise pollution on the spatial distribution of populations remains understudied. The aim was to assess the factors shaping the distribution pattern of an acoustic predator (long-eared owl *Asio otus*) in an urban–farmland matrix. We hypothesized that the probability of an acoustic predator occurring decreases with growing nocturnal noise emission. This owl survey was conducted in Kraków (S Poland) on 79 randomly selected sample plots (1 km × 1 km). Six habitat variables (area of parks, woodlands, grassland, arable land, habitat diversity index, and noise pollution) were identified and correlated with the probability of the species' occurrence. Proximity to pedestrian routes and roads, habitat fragmentation, and noise intensity was also defined at nest sites and random sites. Long-eared owls occurred on 37% of the sample plots. Occupied plots had a greater area of grassland and arable land as well as a lower level of noise pollution than the unoccupied ones. A multivariate model revealed that area of grassland and nocturnal noise emission was significantly correlated with the probability of long-eared owls occurring and that the high probability of occurrence recorded on plots with large areas of grassland was reduced by noise pollution. The noise intensity recorded at nest sites was also significantly lower than at random sites. This study suggests that apart from habitat factors, the distribution of acoustic predators in an urban matrix is driven by noise pollution. This highlights the importance of proper landscape management, that is, maintaining large grassland areas and preventing noise from increasing within them.

Key words: noise pollution, nocturnal predator, road effect, species distribution, urban ecology, urban effect.

In the last 100 years the human population has risen very rapidly and is putting unprecedented pressure on wildlife (Czech et al. 2000; Wittemyer et al. 2008). This ever larger number of people requires more and more food (Daily et al. 1998), which entails expanding the area of farmed land or intensifying crop cultivation. This, in turn, leads to changes in the farmland landscape structure (Tilman et al. 2011; Su et al. 2014), depriving it of microhabitats and key elements of the landscape that are indispensable for many species (McLaughlin and Mineau 1995; Aschwanden et al. 2005; Downs et al. 2016; Yahya et al. 2016; Simons et al. 2017). The use of artificial fertilizers and pesticides not only impoverishes the living conditions of plants consumed by or functioning as hosts for a whole range of herbivores (Tang et al. 2014; Broyer et al. 2017); these substances also poison animals directly, an effect that is potentiated at every successive trophic level (Mineau et al. 1999; Gervais et al. 2000). As a consequence, changes in farming practices are causing sensitive farmland species to disappear and a general decline in biodiversity (Leptich 1994; McLaughlin and Mineau 1995; Melman et al. 2008; Simons et al. 2017).

This diminishing biodiversity of the agricultural landscape is affecting a great many systematic groups (McLaughlin and Mineau 1995; Simons et al. 2017): plants (Tang et al. 2014), insects (Duelli et al. 1999), amphibians (Kolozsvary and Swihart 1999), birds (Gibbs 2000; Parris and Schneider 2009), and mammals (Butet and

Leroux 2001; Hodara and Poggio 2016). Predators are exceptionally sensitive to changes in the farming environment; reacting strongly to variations in the species composition and numbers of prey (Korpimaki and Norrdahl 1991; Leptich 1994; Aschwanden et al. 2005); the disappearance of foraging habitats, perching, and nesting sites (Gibbs 2000; Aschwanden et al. 2005; Yahya et al. 2016); as well as the toxic action of pesticides and other contaminants (Mineau et al. 1999; Geduhn et al. 2016).

A serious threat to the wildlife of farmland landscapes is urban sprawl onto former farmland (Czech et al. 2000; Mcdonald et al. 2008; Jokimäki and Suhonen 2016), reducing and fragmenting habitat area (Trombulak and Frissell 2000; Su et al. 2014). In addition, socio-economic changes are turning villages close to towns and cities into residential areas, with a concomitant decline in their originally rural character and the species associated with them (Ciach 2012; Sushinsky et al. 2013). Urban areas are also sources of air pollution and rodenticides, which accumulate in the bodies of animals (Esselink et al. 1995; Berglund et al. 2011; Geduhn et al. 2016). The pressure of human beings and their pets disturbs wild animals (Hathcock 2010; Cavalli et al. 2016), and artificial lighting disrupts biological rhythms (Da Silva et al. 2015) and causes disorientation, particularly important during migration periods (Longcore and Rich 2004). The urban road network is another factor with a deleterious effect on nature (Trombulak and Frissell 2000), which leads to habitat fragmentation, limits the movements of terrestrial animals (Kolozsvary and Swihart 1999; Ascensão et al. 2017), and forces birds to occupy larger territories (Redpath 1995; Trombulak and Frissell 2000). Moreover, roads are lit up at night (De Molenaar and Sanders 2006), and the traffic on them is a source of air pollution (Esselink et al. 1995; WIOŚ 2014) and causes roadkill (Trombulak and Frissell 2000; Hager 2009).

Among the dangers to the farming landscape that have not received so much attention are the noise and vibrations emitted by the road infrastructure passing through farmland (Parris and Schneider 2009; Ciach and Fröhlich 2017) and also by farming activities (Kropsch and Lechner 2016). Noise is one of the more important factors leading to the homogenization of wildlife (Proppe et al. 2013; Ciach and Fröhlich 2017), as it attenuates acoustic signals and raises the energy expenditure that animals incur when they communicate with each other (Lengagne and Slater 2002; Parris and Schneider 2009). Songbirds are seriously endangered by noise, as they use acoustic signals to establish boundaries of and maintain territories, and to find mates (Parris and Schneider 2009; Nemeth et al. 2013; Proppe et al. 2013). Predators like most species of bats (Schaub et al. 2008; Siemers and Schaub 2011) and owls (Delaney et al. 1999; Mason et al. 2016), which detect their prey acoustically, are another group of animals endangered by noise. Because owls use their hearing to locate and grasp their prey (Mikkola 1983), they are less efficient hunters where ambient noise levels are high (Delaney et al. 1999; Mason et al. 2016). This may compel them to abandon their breeding territories (Hindmarch et al. 2012) or to avoid seemingly suitable habitats (Silva et al. 2012).

The influence of road infrastructure on owls in the farmland landscape remains poorly investigated (Hindmarch et al. 2012; Silva et al. 2012; Scobie et al. 2014), and there are but a handful of papers examining the negative impact of noise on birds in open terrain (Parris and Schneider 2009). Nonetheless, noise may be a more pressing problem in the farming landscape than in woodland areas because the former has thinner distribution of trees, which effectively absorb noise (Fang and Ling 2005; Martínez-Sala et al. 2006). Moreover, farmland habitats may suffer from noise produced by agricultural machinery (Kropsch and Lechner 2016) and increasing traffic in rural areas in the proximity of cities (Ciach 2012).

Long-eared owl *Asio otus* is widely distributed in the northern hemisphere and has a large population size (BirdLife International 2016). The original habitats of this species are forest steppes (Mikkola 1983; Barashkova et al. 2013), from which population expanded into farming landscapes, sparse woodlands, and human-dominated habitats (Henrioux 2000, 2002; Martínez and Zuberogoitia 2004; Aschwanden et al. 2005), including towns, cities, and their suburbs (Zhang et al. 2009; Göçer 2016; Milchev and Ivanov 2016). In Poland, first records of long-eared owl nesting in towns and cities come from the 19th century and presently it is a widespread breeding and wintering bird in urban environments of the country (Tomiałojć and Stawarczyk 2003; Dziemian et al. 2012; Turzanska and Turowicz 2014). Long-eared owl is considered as a food-specialist, feeding mainly on voles (Mikkola 1983; Korpimaki and Norrdahl 1991). However, it shows dietary plasticity and remarkable spatial and temporal variation in food composition depending on food availability and abundance (Bertolino et al. 2001; Romanowski and Zmihorski 2008; Birrer 2009; Mori et al. 2014; Mori and Bertolino 2015). The diet of urban long-eared owl may include rats (Laiu and Murariu 1998; Pirovano et al. 2000), birds (Kiat et al. 2008; Göçer 2016), bats (Zhang et al. 2009; Tian et al. 2015), and insects (Ciach 2006; Birrer 2009). Occasionally, carrion consumption may enlarge the trophic spectrum (Mori et al. 2014).

In most of its range the long-eared owl is a typical farmland species (Glue 1977; Mikkola 1983), the distribution of which depends closely on the intensification of agriculture (Martínez and Zuberogoitia 2004; Aschwanden et al. 2005; Moreno-Mateos et al. 2011). However, the distribution of this species in urbanized habitats and the factors affecting this are poorly understood. The aim of this study was to assess the environmental parameters shaping the distribution pattern of long-eared owls in an urban–farmland matrix. We hypothesized that the availability of primary foraging and nesting habitats, which in the case of long-eared owls are farmland and wooded areas, respectively, would increase the probability of this species occurring. However, we also assumed that noise—intense and constantly present in urban environments—would be the factor responsible for reducing the probability of their occurrence. Moreover, we predicted that noise levels would influence nest-site preferences and that the owls would select sites with low noise intensity.

Materials and Methods

Study site

This study was carried out in the city of Kraków (southern Poland, 50°05′ N, 19°55′ E), which covers an area of 327 km^2 and has a population density of 2,331 persons/km^2 (GUS 2016). Kraków is characterized by a broad urbanization gradient—from the densely built-up city center, through extensive suburbs with a moderate number of buildings to the scattered buildings typical of a farmland landscape (Figure 1). The human settlements cover 6% of the study area, which range from the compact, continuous structures that cover the ground completely through taller and shorter blocks of flats to detached and semi-detached houses, with varying amounts of greenery in between (MIIP 2016).

Open areas make up 37% of the study area, that is, arable land (14%), spontaneous ruderal communities (13%), meadows and pastures (8%), and wetland vegetation (2%). Open habitats are situated primarily on the city's outskirts, although there are also some nearer the city center, surrounded by densely built-up areas. Urban

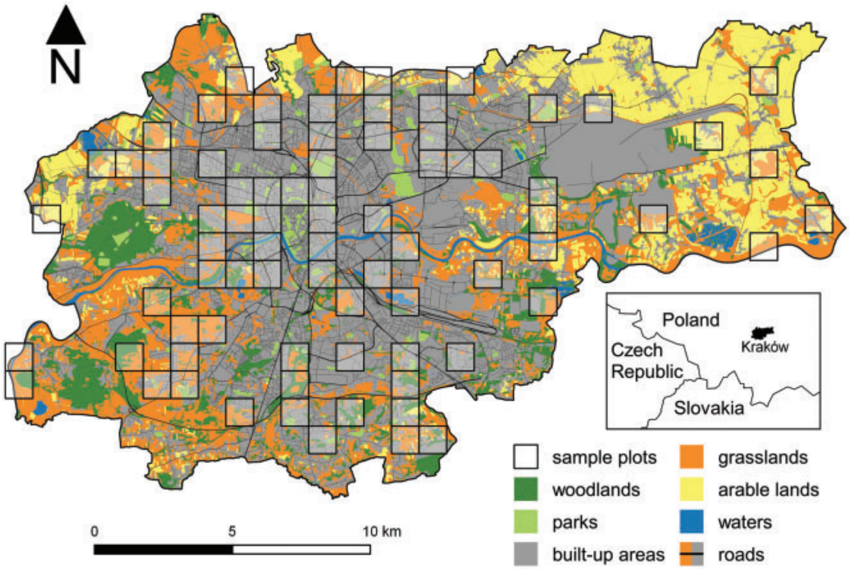

Figure 1. Study area, main habitat types, and distribution of sample plots in Kraków (S Poland) used for assessing habitat variables that influence the distribution pattern of long-eared owls *Asio otus* in an urban environment.

greenery (47%) consisting of native and non-indigenous species in various spatial arrangements, forms of management, and stages of succession, includes gardens (14%), squares, road verges and playgrounds (10%), allotments and orchards (4%), parks and cemeteries (3%), and other green areas (15%). Forests and natural woodlands constitute 11% of the city area: natural and semi-natural scrub (5%), deciduous and mixed forests (4%), and damp, riparian forests, and transformed tree stands (2%) (Dubiel and Szwagrzyk 2008). Surface waters make up 1% of the study area, and the principal waterway is the River Wisła (Vistula); 6 medium-sized tributaries and numerous smaller watercourses flow into the Wisła within the city limits (MIIP 2016). The city's roads and railway lines make up 4% of its overall area (Dubiel and Szwagrzyk 2008). The quality of air in Kraków is among the worst in Europe, containing high levels of suspended particulate matter, nitrogen dioxide and benzo(alpha)pyrene (WIOŚ 2014; AQIE 2015).

Sample plot selection and fieldwork

Seventy-nine sample plots were surveyed during the long-eared owl's breeding periods in 2015 and 2016 (Figure 1). Initially, the city was divided into 389 1 km × 1 km squares from which the sample plots were selected at random using Quantum GIS software (QGIS 2013). The grid of squares was based on a point with coordinates 50° N and 20° E. According to recommendation provided by Hardey et al. (2006), 2 surveys of territorial adults were carried out during the breeding season: early (01–31.03) and late (01–30.04). A period of at least 2 weeks had to elapse between consecutive surveys. Counting using the standard mapping technique was combined with playback dedicated to owl surveys (Bibby et al. 1992; Zuberogoitia and Campos 1998). Two-minute recordings of courtship and contact calls were played back through a 3-W loudspeaker at playback points. On completion of playback, 3 min was allowed to elapse to enable the birds to react (territorial calls). Because playback methods in long-eared owl surveys are not very effective (Zuberogoitia and Campos 1998; Martínez et al. 2002), recordings of calls of potentially co-occurring or competing owl species (little owl *Athene noctua* and tawny owl *Strix aluco*, respectively) were played back after long-eared owl recordings (Mikkola 1976; Nilsson 1984; Romanowski 1988). This causes the birds to fly over a loudspeaker or provokes loud alarm calls/calls of young birds [in the present work 72.4% ($N = 29$) of all observations were visual confirmations of birds turning up in the vicinity of the observer; 44.8% ($N = 29$) of this visual records took place during playback of tawny owl calls].

The standard version of the method adapted for owl surveys in natural habitats advises locating the playback (voice stimulation) point at a distance of 250–500 m from one another (Zuberogoitia and Campos 1998; Rodriguez et al. 2006). However, for urban environments these recommendations have to be modified because of the noise level, which may limit detectability; therefore, the distribution of playback points has to be sufficiently dense to ensure a high level of bird detectability. Based on field experiments into the audibility of voice playbacks in urban conditions (Fröhlich and Ciach, 2017), a distance of 300 m between playback points was applied to ensure complete coverage of survey area (this meant that the maximum distance between the observer and a potential calling owl locality was 150 m). A systematic grid of 13 playback points was assigned on each sample plot (grid of playback points was situated obliquely in relation to plot border). The actual conditions on the ground (existing buildings, walls, fences, etc.) meant that the real playback points had to be displaced to the nearest convenient site. The playback work was done between the hours of midnight and 04:00 CET (when road traffic intensity is the lowest) exclusively in rain-free and windless weather. The plots were walked at an average speed of 2 km/h. A single survey of a study plot took around 4 h and all bird records and their activity were entered on the maps. In order to locate nesting sites, additional surveys in all territories recorded on sample plots were conducted in May–June. Observers searched the area for potential nesting sites, looking for nests or young. The precise locations of nests were established using a GPS device.

Environmental variables at the landscape-scale

The habitat parameters were defined within the boundaries of the sample plots based on existing spatial database resources using

Geographic Information System tools (Table 1). The total surface areas of the 4 habitat types of primary importance for long-eared owl were calculated using the polygon vector layer of the atlas of the real vegetation of Kraków (UMK 2012), which is the effect of fieldwork done in 2006 (Dubiel and Szwagrzyk 2008). The atlas categorizes the city area into 58 habitat types, which have been allocated to one of the 4 primary habitat types. A separate polygon vector layer was created for each of these. Parks (PARK) included parks and cemeteries; woodlands (WOODLAND) included natural forests and woodlands, consisting of deciduous and coniferous tree species, mixed stands, and naturally growing shrubs; grassland (GRASSLAND) included meadows, pastures, uncultivated and fallow land, rock vegetation, swards, heaths, and the communities of trampled areas; finally, arable lands (ARABLE_LAND) included fields used for agricultural production. Each of these layers was reduced by the layer containing the outlines of buildings, roads, and the layer of surface waters (WODGiK 2015), which yielded the actual surface area of a given habitat type.

The Shannon–Wiener habitat diversity index (HABITAT_DIVERSITY) was calculated on the basis of the proportions of the particular habitats within the boundaries of the sample plots. Ten types of habitat were used for this purpose: parks (parks and cemeteries), squares (squares, road verges, and playgrounds), gardens (gardens, allotments, and orchards), managed greenery of commercial properties, natural forest (deciduous and coniferous forest, mixed woodland, and naturally growing shrubs), grassland (meadows, pastures, uncultivated and fallow land, rock vegetation, swards, heaths, and the communities of trampled areas), arable lands (UMK 2012), surface waters (rivers and bodies of water) (WODGiK 2015), built-up areas (total area of buildings), and roads (total area roads and railways) (WODGiK 2015).

The nocturnal noise emission parameter (NOISE) was determined from the map of road noise emission (MIIP 2016). The mean noise class weighted by its range area was calculated for every sample plot. Noise values during the hours of darkness were used for these calculations. The map shows the noise level expressed in 9 classes of sound intensity (dB) (1 to <45, 2 to 45–50, 3 to 50.1–55, 4 to 55.1–60, 5 to 60.1–65, 6 to 65.1–70, 7 to 70.1–75, 8 to 75.1–80, 9 to > 80). The map was compiled jointly by the Provincial Environmental Conservation Inspectorate in Kraków and the Kraków City Council based on the data collected in 2012 (MIIP 2016). The map shows the data in the form of a vector layer.

Local-scale approach (nest-site selection)

To evaluate the impact of noise on nesting site selection by long-eared owls we compared noise intensities between nests and reference locations (NOISE_NEST). For these measurements we used detailed location data of nests found in 18 territories. Reference locations were randomly selected within each of these territories and represented potentially suitable long-eared owl nesting sites. First, all patches of primary foraging habitat (grassland) up to 500 m from a given nest were identified in each territory (the maximum distance between nests and the nearest grassland patch was 485 m). Then, around these potential foraging areas were delineated 500 m buffers in which the reference location was selected at random. Since long-eared owls depend heavily on large nests constructed by other birds (mainly corvids), these random locations were shifted to the nearest existing potentially suitable nest (habitats were surveyed in order to find the nest nearest to the reference location). We considered large open nests of corvids to be suitable nesting sites for long-eared owls (Mikkola 1983; Henrioux 2002; Lövy and Riegert 2013).

Nocturnal noise intensity at occupied nest sites and randomly selected nest sites (NOISE_NEST) was measured using a portable sonometer accurate to 0.1 dB. To exclude the effect of variation in traffic volume, measurements were made solely within a strictly defined period of the day, that is, when road traffic was moderate (21:00–00:00 h), excluding moments with extreme noise picks (e.g., plane flight, ambulance siren). Noise measurements were made pairwise, with a 15 min interval at most between the measurements at the nest and the corresponding reference location. This variable was expressed as the mean value of a single point in time measurements taken in 4 directions at right angles to each other.

Since noise level could be correlated with the presence of urban infrastructure such as roads and pedestrian routes, this effect needed to be separated from the presence of such structures. Therefore, for each of the occupied nests and randomly selected nest sites we measured the distance from the nearest (1) route used by pedestrians, that is, pavements, pedestrian routes (PAVEMENT) and (2) road used by motor vehicles (ROAD). The measurements were made on the basis of orthophotographs from 2015 (GUGiK 2016) accurate to 1 m.

To control the proper selection of reference locations, we calculated the total area of grassland around the occupied nests and randomly selected nest sites (GRASSLAND_NEST), which is a major landscape-scale driver of the species' occurrence, and the perimeter-to-area ratio as a measure of the shape and fragmentation of primary foraging habitat (GRASSLAND_GEOMETRY). These parameters

Table 1. Habitat and environmental parameters measured at the landscape-scale (in sample plots situated in an urban environment) and the local-scale (at nest sites of long-eared owls *Asio otus* and randomly selected nests)

Variable	Code	Unit	Data source
LANDSCAPE-SCALE			
Area of parks	PARK	ha	UMK (2012)
Area of woodland	WOODLAND	ha	UMK (2012)
Area of grassland	GRASSLAND	ha	UMK (2012)
Area of arable land	ARABLE_LAND	ha	UMK (2012)
Habitat diversity index	HABITAT_DIVERSITY	index	UMK (2012); WODGiK (2015)
Nocturnal noise emission	NOISE	class	MIIP (2016)
LOCAL-SCALE			
Total grassland area within 900 m buffer	GRASSLAND_NEST	ha	UMK (2012)
Grassland perimeter-to-area ratio within 900 m buffer	GRASSLAND_GEOMETRY	ratio	UMK (2012)
Distance between the nest and the nearest pedestrian route	PAVEMENT	m	GUGiK (2016)
Distance between the nest and the nearest road	ROAD	m	GUGiK (2016)
Nocturnal noise intensity	NOISE_NEST	dB	Fieldwork

were calculated for a buffer of 900 m radius around the nests and random sites based on the average home-range radius of long-eared owls breeding in urban areas (Lövy and Riegert 2013).

Data analysis

Mean (±SD) and median (with quartiles) values of each environmental variable for plots (1) occupied and (2) unoccupied by long-eared owls were calculated, the differences between the 2 groups being analyzed with Mann–Whitney's *U*-test. To control for multicollinearity between environmental variables, a Spearman rank correlation matrix of all the variables was plotted (the correlation was <0.5 for all variable pairs). Spatial autocorrelation of plots occupied by long-eared owls was assessed with Moran's tests (Rangel et al. 2010). We detected no evidence of spatial autocorrelation (Moran's *I* was close to zero for all separation distances and semi-variance did not increase with lag distance).

Factors determining the probability of long-eared owls occurring in an urban environment were investigated using a generalized linear model with binomial error distribution (Bolker et al. 2009). For this purpose we used environmental variables potentially explaining the presence of long-eared owls and took the area of 4 primary habitat types (PARK, WOODLAND, GRASSLAND, ARABLE_LAND), the habitat diversity index (HABITAT_DIVERSITY), and nocturnal noise emission (NOISE) to be explanatory variables. Then, a logistic regression model (with species absence/presence as a dichotomous dependent variable) was run for the variables, indicated in the linear model as being of major importance for the probability of long-eared owls occurring, in order to detect threshold values determining the species' presence.

Differences at the nest-site scale were analyzed using Student's paired *t*-test. We regarded total area of grassland (GRASSLAND_NEST) and its perimeter-to-area ratio (GRASSLAND_GEOMETRY), distance from the nearest pedestrian route (PAVEMENT), distance from the nearest road (ROAD) and noise intensity (NOISE_NEST) as explanatory variables. The statistical procedures were performed using Statistica 12 software (StatSoft Inc. 2014).

Results

Long-eared owls were recorded on 36.7% of the sample plots ($N = 79$). Occupied plots contained significantly more grassland and marginally more arable land (Table 2). The level of noise on the occupied plots was significantly lower than on the unoccupied plots (Table 2). Neither the area of parks and woodlands nor habitat diversity differed significantly between occupied and unoccupied plots (Table 2).

The multivariate model revealed that area of grassland and nocturnal noise emission were significantly correlated with the probability of long-eared owls occurring (Table 3). A high such probability recorded on a plot with a large area of grassland was reduced by nocturnal noise emissions (Figure 2). This model indicates that an increase in noise intensity to ∼50–60 dB (3–4 noise class) lowered the probability of long-eared owls occurring to ∼0.4–0.6 where large areas of grassland (80–100 ha) were available. Where the area of grassland was small (<20 ha), even a small increase in noise intensity strongly reduced the likelihood of long-eared owls occurring (Figure 2).

Noise levels at the nest sites were significantly lower than at the random sites (Table 4). The distance to the nearest pedestrian route or road did not differ significantly between nests and random sites. The total area of grassland and the grassland perimeter-to-area ratio did not differ significantly between nest sites and random sites, although the *P* value of the latter variable was approaching the significance level (Table 4).

Discussion

We have shown that the probability of long-eared owls occurring in urban environments is positively correlated with the availability of their primary foraging habitat (grassland) but is negatively correlated with ambient noise intensity. Earlier papers hinted at the adverse effects of the road network and its associated traffic on the occurrence of owls (Hindmarch et al. 2012; Silva et al. 2012), but they did not analyze ambient noise levels in the context of owl occurrence. Since these birds use their hearing to locate prey (Mikkola 1983), they will need more time to do so when noise levels are high, and hunting efficiency will be impaired (Delaney et al. 1999; Mason et al. 2016). Where noise is short-lived, owls can break off hunting until it dies down (Delaney et al. 1999; Scobie et al. 2014). But where noise is

Table 3. Generalized linear model predicting the probability of long-eared owls *Asio otus* occurring in an urban environment (Kraków, S Poland; for parameters, see Table 1); significant values in bold

	Estimate	SE	Wald's stat.	95% CI	*P*
INTERCEPT	−2.394	2.254	1.13	−6.812 to 2.024	0.288
PARK	0.003	0.040	0.01	−0.075 to 0.082	0.933
WOODLAND	0.005	0.024	0.04	−0.042 to 0.051	0.848
GRASSLAND	0.038	0.017	4.88	0.004 to 0.071	**0.027**
ARABLE_LAND	−0.007	0.021	0.12	−0.048 to 0.034	0.725
HABITAT _DIVERSITY	1.820	1.131	2.59	−0.398 to 4.037	0.108
NOISE	−1.043	0.475	4.82	−1.974 to − 0.112	**0.028**

Table 2. Descriptive statistics and Mann–Whitney's *U*-test results for landscape scale variables analyzed in the study plots occupied and unoccupied by long-eared owls *Asio otus* in an urban environment (Kraków, S Poland; for parameters, see Table 1); significant values in bold

Variable	Occupied ($N = 29$)				Unoccupied ($N = 50$)				Z_c	*P*
	Mean	SD	Median	Quartiles range	Mean	SD	Median	Quartiles range		
PARK	3.9	6.1	1.4	0.0–5.9	5.1	8.3	2.4	0.1–6.4	−0.96	0.337
WOODLAND	10.2	12.1	7.8	1.7–14.6	8.5	12.0	3.6	0.1–10.2	1.33	0.183
GRASSLAND	30.1	18.8	30.2	17.4–41.7	18.1	17.9	10.1	4.3–25.9	2.71	**0.007**
ARABLE_LAND	8.9	11.3	2.6	0.0–15.4	8.0	17.1	0.0	0.0–4.4	1.98	**0.048**
HABITAT_DIVERSITY	1.6	0.3	1.6	1.4–1.7	1.5	0.3	1.6	1.4–1.7	0.70	0.486
NOISE	1.6	0.6	1.3	1.1–2.2	2.1	0.7	2.0	1.6–2.6	−2.84	**0.004**

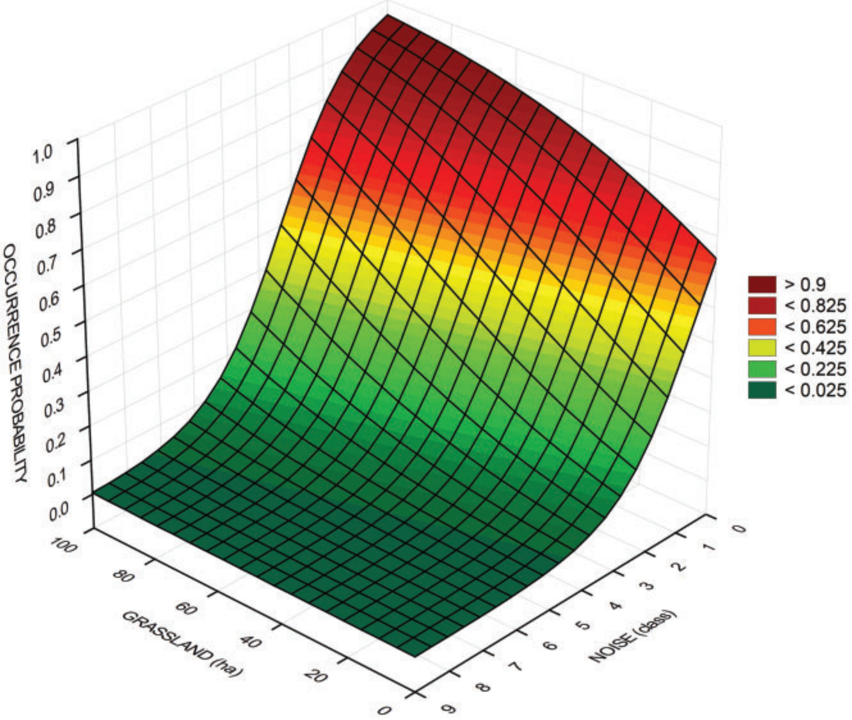

Figure 2. Logistic regression model of the probability of long-eared owls *Asio otus* occurring, the area of grassland and nocturnal noise emission (see "Materials and Methods" section, Table 1) in an urban environment (Kraków, S Poland).

Table 4. Descriptive statistics and paired Student's *t*-test results for local-scale variables analyzed at the nest sites of long-eared owls *Asio otus* and randomly selected nest sites in an urban environment (Kraków, S Poland; for parameters, see Table 1); significant values in bold

Variable	Nest site ($N = 18$)		Random site ($N = 18$)		*t*	*P*
	Mean	SD	Mean	SD		
GRASSLAND_NEST	101.9	65.2	100.2	96.5	0.09	0.930
GRASSLAND_GEOMETRY	0.04	0.03	0.05	0.04	−1.98	0.064
PAVEMENT	12.50	15.34	12.72	15.35	−0.04	0.965
ROAD	77.17	89.76	50.11	50.37	1.08	0.297
NOISE_NEST	42.6	3.2	46.7	4.8	−5.19	**0.000**

continuous, such as that generated by road traffic, owls may avoid areas close to roads or compensate for a habitat's poorer quality by increasing its area, and that may imply a lower population density (Silva et al. 2012).

This is the first paper to analyze simultaneously the effect of noise in conjunction with the very presence of urban infrastructure (roads and pedestrian routes) on the distribution of owl nests. Earlier papers examining the influence of road networks on owls did not explain which road effects were key to limiting owl populations (Hindmarch et al. 2012; Silva et al. 2012; Scobie et al. 2014). A dense road network in owl habitats has other negative impacts, such as increased roadkill (Erritzøe 1999; Trombulak and Frissell 2000; Hager 2009), air pollution reducing individual condition (Esselink et al. 1995; Trombulak and Frissell 2000; Berglund et al. 2011), greater human pressure disturbing birds (Hathcock 2010; Cavalli et al. 2016), and habitat fragmentation, which may require owls to occupy larger territories or to avoid highly fragmented habitats (Redpath 1995; Trombulak and Frissell 2000; Grossman et al. 2008). Our results strongly suggest that noise is a road effect shaping the spatial distribution of owls, as this may reduce hunting efficiency (Delaney et al. 1999; Mason et al. 2016) and/or communication (Lengagne and Slater 2002) in noisy areas.

Our research shows that long-eared owl occurrence is strongly positively correlated with the area of primary foraging habitat—grassland. The original habitat of long-eared owls was forest steppes (Mikkola 1983; Barashkova et al. 2013), which in Europe have been replaced by farming landscapes, which provide suitable hunting habitats (Getz 1961; Mikkola 1983; Holt 1997; Henrioux 2000) and nesting sites (Mikkola 1983; Henrioux 2002; Lövy and Riegert 2013). The present work also indicates that grassland fragmentation has little negative impact on nest site selection in long-eared owls. The species' original habitat (forest steppes) is a mosaic of open areas and woodland; consequently, the scattered/fragmented meadows may be a suitable hunting habitat (Mikkola 1983; Henrioux 2000; Lövy and Riegert 2013). However, the loss of habitat integrity could be a serious threat to some predators. Several studies indicate that woodland owl species are sensitive to habitat fragmentation (Galeotti 1994; Redpath 1995; Grossman et al. 2008).

Although long-eared owls often nest in wooded areas (Holt 1997; Henrioux 2000, 2002), our results indicate that such habitats (woodlands and parks) are of minimal significance for the occurrence of this species. This may well be due to this owl's flexibility when it comes to choosing a nest site (Mikkola 1983; Holt 1997; Rodriguez et al. 2006). Corvids—the prime suppliers of nests for long-eared owls (Mikkola 1983; Henrioux 2002; Lövy and Riegert 2013)—nest fairly frequently in urban areas: they are present in woodlands and parks, as well as in all types of urban greenery (Jokimäki and Suhonen 2016). Wooded areas, however, are probably an unsatisfactory hunting habitat for this species (Getz 1961; Mikkola 1983; Henrioux 2000). Moreover, telemetric studies have shown that foraging birds avoid urban greenery like parks, which in their structure (Lövy and Riegert 2013)—thinly distributed trees and plenty of grassland—to some extent resemble forest steppes, the natural biotopes of long-eared owls (Mikkola 1983; Barashkova et al. 2013). It may be difficult for owls to hunt in parks because of disturbance by humans and their dogs (Hathcock 2010; Cavalli et al. 2016).

The regression model we have used in our work indicates that the negative impact of noise on the probability of occurrence of long-eared owls is mitigated if a large area of grassland is available. The owls can refrain from hunting during the noisiest times of the night or else search for foraging areas more distant from sources of noise (Delaney et al. 1999; Scobie et al. 2014; Mason et al. 2016). Since number and area of noise-free sites is relatively low and these are scattered within the city owls are forced to locate territories only in suitable habitat patches (Galeotti 1994). This may be an important reason why owls have smaller territories in urban areas (Lövy and Riegert 2013). On the other hand, if only small areas of hunting habitat are available, even a small increase in noise levels will drastically reduce the probability of these owls being present there. At sites affected by high noise levels, long-eared owls are presumably unable to compensate for an impoverished basic habitat by turning to other habitats where prey is not so easy to come by. This result underscores the strongly adverse reaction of habitat specialist species to noise.

Our findings suggest that noise intensity may also reduce the number of potential nesting sites of long-eared owls. Begging calls, frequent in young long-eared owls, stimulate the parent birds to hunt and enable them to locate their scattered fledglings (Mikkola 1983). High noise intensities may reduce the effectiveness of communication between family members and in theory, therefore, may tend to weaken family bonds and lower reproductive output. Continuous noise around the nest might hinder young birds from acquiring the ability to use their hearing when hunting (Mikkola 1983; Mason et al. 2016). In addition, noise can interfere with the vocalizations of adult birds when they are establishing territories; in long-eared owls this may be particularly serious given that their territorial calls are relatively quiet (Mikkola 1983; Zuberogoitia and Campos 1998).

Although disturbance by people can elicit adverse reactions in owls (Cavalli et al. 2016), and in natural environments can even cause these birds to abandon their nesting sites (Hathcock 2010), our results do not indicate that the proximity of pedestrian routes is of any importance in nest-site selection by long-eared owls. Most of their nests are sited high up in trees, so they are probably at a safe distance from people (Glue 1977; Mikkola 1983; Rodriguez et al. 2006). Distance to roads, which, if short, potentially raises the risk of roadkill (Erritzøe 1999; Trombulak and Frissell 2000; Hager 2009), was of no importance either as regards nest-site selection by these owls. Again, nesting on trees which are located near roads is not likely to lead to collisions with vehicles because the birds fly to and from their nests at heights well above the traffic. However, long-eared owls do become potential roadkill victims mainly during their zig-zag foraging flights low over the ground, when they are hunting for rodents (Mikkola 1983) or during occasional feeding on roadkills (Erritzoe et al. 2003; Mori et al. 2014).

Roads may potentially influence prey resources available to owls as they have either positive effects or no effect on small mammals abundance and distribution (Fahrig and Rytwinski 2009). Moreover, traffic noise is not considered as a factor leading to avoidance of the roads by small mammals (McGregor and Bender 2008; Fahrig and Rytwinski 2009). Therefore, differences in food resources in the vicinity of roads should not be considered as a driver of owl occurrence. Moreover, considering relatively high dietary plasticity of long-eared owl, which may switch to alternative prey (e.g., Birrer 2009; Mori and Bertolino 2015), the reduced possibility of successful hunting rather than food availability should be responsible for avoidance of areas with high noise intensity.

In summary, this study has demonstrated that apart from habitat factors, long-eared owl distribution is associated with noise pollution. Our results suggest that the probability of long-eared owls occurring at a site is determined mainly by the area of grassland, this owl's preferred foraging habitat, but also by nocturnal noise emissions, which may reduce hunting efficiency. This study adds to the growing body of evidence that noise has a negative impact on owl assemblages and highlights the importance of appropriate farmland management, that is, the maintenance of large grassland patches and the suppression of noise within them.

Acknowledgements

We wish to express our gratitude to Julia Barczyk, Mateusz Bernat, Mirosław Brzozowski, Katarzyna Bul, Anna Chomczyńska, Mateusz Dutko, Mateusz Górniak, Joanna Jaszczyk, Mirosław Kata, Gabriela Kuglin, Magdalena Kukla, Krzysztof Kus, Przemysław Lelito, Jacek Maślanka, Cezary Mozgawa, Patrycja Pisarska, Karolina Ptak, Monika Ptak, Fabian Przepióra, Maciej Pyzik, Zuzanna Sidorowicz, Urszula Sieńkow, Anna Sitarz, Katarzyna Staszyńska, Daria Strączyńska, Teresa Strączyńska, Agata Uliszak, Paweł Wieczorek, Jakub Wyka, Błażej Zamojski, and Anna Zięcik for their help with the fieldwork. We want to thank anonymous reviewers for their constructive comments on the manuscript. Financial support for this study was provided by the Polish Ministry of Science and Higher Education by statutory grant (DS 3404).

Conflict of interest

The authors declare that they have no conflict of interest.

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