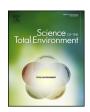
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Escape behaviour of birds in urban parks and cemeteries across Europe: Evidence of behavioural adaptation to human activity



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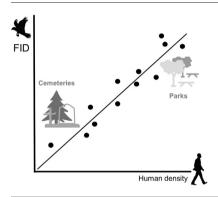
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HIGHLIGHTS

• We calculated the bird flight initiation distance (FID) in parks and cemeteries.

- Birds allowed people closer in cemeteries than in parks.
- The pattern was persistent even when focusing on FID of the most common bird species.
- FID was negatively associated to size of parks/cemeteries and positively to human density.
- The escape behaviour of urban birds is adaptable to human behaviour (pedestrians speed).

GRAPHICAL ABSTRACT



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ABSTRACT

Urban environments are very heterogeneous, and birds living in the proximity of humans have to adapt to local conditions, e.g. by changing their behavioural response to potential predators. In this study, we tested whether the escape distance of birds (measured as flight initiation distance; FID) differed between parks and cemeteries, areas characterized by different microhabitat conditions and human conduct, that are determinants of animal behaviour at large spatial scales. While escape behaviour of park populations of birds was often examined, cemetery populations have not been studied to the same extent and a large-scale comparison is still missing.

Overall, we collected 2139 FID estimates for 44 bird species recorded in 79 parks and 90 cemeteries in four European countries: Czech Republic, France, Italy and Poland. Mixed model procedure was applied to study escape behaviour in relation to type of area (park or cemetery), environmental characteristics (area size, coverage by trees, shrubs, grass, chapels, tombstones, flowerbeds, number of street lamps) and human activity (human density, pedestrians speed and ratio of men/women).

Birds allowed people closer in cemeteries than in parks in all countries. This pattern was persistent even when focusing on intraspecific differences in FID between populations of the most common bird species. Escape distance of birds was negatively correlated with the size of parks/cemeteries, while positively associated with tombstone coverage and human density in both types of habitat. Our findings highlight the ability of birds to adapt their behaviour to different types of urban areas, based on local environmental conditions, including the character of human–bird interactions. Our results also suggest that this behavioural pattern may be widespread across urban landscapes.

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1. Introduction

The negative effects of human activity and urbanization on biodiversity were explored in many studies in the last decade (Cardinale et al., 2012; McKinney, 2002; Newbold et al., 2016; Shochat et al., 2010), and one of the most important issues is related to the biotic homogenization of animal communities. The functional or biotic homogenization is characterized by increasing similarities across communities in space and time (Devictor et al., 2007; McKinney, 2006; McKinney and Lockwood, 1999), promoting similar communities, with dominant species among different urban locations (Møller, 2012). On the other hand, animals, including birds, which are able to live in the proximity of humans may gain significant benefits from sympatry with human in terms of favourable microclimatic conditions (Oke, 1973), higher food availability (Jokimäki et al., 2014; Sol et al., 2013), and lower predation risks (Díaz et al., 2013; Ditchkoff et al., 2006; Møller, 2012).

Despite urban environments may first appear homogenous, humanassociated areas offer a wide spectrum of different microhabitat types. Within urban environments, diversity of birds tends to decrease in well-urbanized and densely built-up areas (Clergeau et al., 2001; Fernández-Juricic and Jokimäki, 2001; Jokimäki, 1999; Stagoll et al., 2012), but can be high in green areas with parks and cemeteries recognized as potential urban biodiversity hotspots (Čanády and Mošanský, 2017; Croci et al., 2008; Tryjanowski et al., 2017). Urban parks and other forms of urban greenery constitute important refuges for wildlife in an increasingly urbanized world (Alvey, 2006). Urban parks can provide a resource for maintaining or increasing urban biodiversity, especially for bird species (Chiesura, 2004; Schütz and Schulze, 2015; Strohbach et al., 2009). Similarly, cemeteries, despite less studied, can constitute a source of suitable habitat for many birds (Banaszak-Cibicka et al., 2016; Bonnet et al., 2016; Łopucki and Kitowski, 2016; Tryjanowski et al., 2017). For instance, park and cemetery infrastructures (e.g. buildings, monuments, lamps, flowerbeds, etc.), and diverse vegetation cover and land use can provide new breeding and foraging opportunities for some species of birds (Germaine et al., 1998; Tryjanowski et al., 2017). Also artificial lights in urban areas can affect many bird species, both by changing light-dark pattern, as well as by attracting insects and the modified local food supplies (Ciach and Fröhlich, 2016; Klem, 2007; Kociolek et al., 2011).

Recently, researchers started to study the behavioural adaptations of animals living in urbanized habitats (Chapman et al., 2012; Møller et al., 2013; Møller and Ibáñez-Álamo, 2012; Samia et al., 2017). Urban habitats are very heterogeneous in environmental conditions, local predator communities, and human activities (Mikula, 2014; Møller and Tryjanowski, 2014). The rural-urban gradient is commonly linked to considerable variation in abundance and species composition of predator communities (Lepczyk et al., 2003; McKinney, 2002). Predation is an important selective agent affecting evolution of adaptive traits, and, hence, success when invading novel environments may depend on flexibility of adjustment of antipredator strategies to local conditions (Jerzak, 2001; Møller et al., 2010; Møller and Ibáñez-Álamo, 2012). Abundance of raptors is often lower in urban than in rural habitats, and, hence, habitat type has a strong effect on wide-scale antipredator behaviour of birds, including shorter flight initiation distances (FID) in urban areas (Díaz et al., 2013). FID is used as a metric reliably quantifying level of risk taking in animals and hence, reflecting the trade-off between costs of premature escape and benefits from staying (Díaz et al., 2013; Kunca and Yosef, 2016; Legagneux and Ducatez, 2013). However, local-specific environmental conditions may have an effect on FID adjustment that can differ even within particular urban habitat types (Bötsch et al., 2017; Fernández-Juricic et al., 2002).

Beside coping with altered predation risk, tolerance to human disturbance seems to be one of the key factors facilitating successful colonization of urban environments, which enables efficient exploitation of local resources, and also saves time and energy, otherwise allocated to unnecessary escape from approaching humans (Blumstein et al.,

2005; Díaz et al., 2013; Møller, 2008; Samia et al., 2017). Escape behaviour is costly, especially if elicited frequently, and urban environments often select for a reduction in antipredator response to human presence (Blumstein et al., 2005; Mikula, 2014; Møller, 2008; Møller et al., 2013; Samia et al., 2017). It has been found that escape behaviour is affected by multiple factors directly related to human activity at specific localities, including density and speed of approaching humans (Blumstein, 2006; Mikula, 2014; Stankowich and Blumstein, 2005). Individuals exposed to long-term higher levels of human density have typically shorter FID which may be linked, for instance, to the process of habituation to repeated human exposure and/or non-random distribution of individuals among sites based on their individual susceptibility to the local level of human disturbance (Blumstein, 2006; Carrete and Tella, 2010; Mikula, 2014). In parks, visitors typically move faster (many people are using parks for sports activities, including running or cycling), are noisier and can have pets with them (it is often not permitted to enter a cemetery with pets). Human pets may pose a significant threat to birds during the breeding season (Díaz et al., 2013; Stankowich and Blumstein, 2005). Hence, birds in parks may exhibit more vigilant behaviour because they are particularly sensitive to increased presence of human pets (Miller et al., 2001). Finally, response of birds to approaching humans can also differ in areas differing in the proportion of men and women. Men are taller on average and, similarly, their body mass tend to be larger than in women (Ogden et al., 2004). Size of potential predators influences perceived threat (Stankowich and Blumstein, 2005), and birds may perceive men as more threatening; human size-FID relationship was, however, only rarely tested (Van Dongen et al., 2005). Hence, investigation of intra- or interspecific differences in risk taking can provide useful information on the ability of birds to adapt to local conditions (Blumstein, 2006; Møller, 2008).

The aim of this study was to test whether bird communities inhabiting European parks and cemeteries differed in their escape behaviour (measured as FID). We hypothesized that differences in abiotic and biotic environmental characteristics can affect responses of birds. We applied a mixed model approach and regression analysis to compare FID between park and cemetery birds, focusing on relative importance of factors, including type of area, category of urbanization, vegetation and human-related structural coverage and human activity pattern, on escape behaviour of birds. Finally, we tested whether FID consistently differs between individuals of the most common species occurring in parks and cemeteries.

2. Methods

2.1. Study areas, environmental characteristics and human activity

Data were collected in four European countries: Czech Republic, France, Italy and Poland, in urban or rural areas. In Czech Republic, the parks and cemeteries were visited within the city of Prague. In France, parks and cemeteries were selected in rural and urban areas of the department of Vienne, and within the city of Poitiers. In Italy, parks and cemeteries were selected in rural and urban areas of Central Italy, in the Marche region, and within the cities of Pesaro, Fano and Urbino. In Poland, parks and cemeteries were selected in rural and urban areas of Central Poland, and within the city of Poznań. Fig. S1 in Electronic Supplementary Material shows the geographic distribution of parks and cemeteries visited in this study for data collection. The distance among parks and cemeteries was always longer than 1 km.

Each park and cemetery was characterized by several variables linked to the vegetation and built-up coverage. Each site was classified into three main categories according to their location, regarding the surrounding landscape as rural, peri-urban and urban. Urban areas included areas with multi-storey buildings, single family houses, roads and parks, while nearby rural areas had open farmland and woodland and did not contain continuous urban elements like multi-storey buildings, family houses, roads and parks. The classification of environments

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