

Breeding habitat selection of urban peregrine falcons (*Falco peregrinus*) in London

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Abstract

Understanding habitat selection by individual animals within their home range is crucial to facilitating their conservation. Peregrine falcon (*Falco peregrinus*) populations are increasingly urbanised, but little is known about their urban habitat use. In this study, we analysed the breeding habitat selection of peregrine falcons in London, United Kingdom, based on nest site locations identified through records of public sightings submitted to an online database between 2003 and 2018. We found peregrines displayed a preference for nesting in proximity to waterbodies, built-up areas and public parks and gardens, while wooded, agricultural and allotments areas were least preferred. We hypothesise that peregrines seek contrasting topography that proves advantageous for hunting in the vicinity of their nests, resulting in their selection of breeding sites within tall buildings that are adjacent to suitable foraging areas. From these findings, we conclude that (i) social drivers such as demand for green spaces and waterbodies near buildings shape peregrine nesting opportunities in the city and (ii) for urban planning to support conservation, we need further understanding of how each type of greenspace may be used differentially by raptors.

Key words: bird diversity, urban peregrine falcon, public sighting, habitat preference, compositional analysis, avifauna

Introduction

Urbanisation filters avian communities and many birds of prey are absent from human landscapes due to their sensitivity to anthropogenic pressures (Marzluff 2001; Chace and Walsh 2006; Seress and Liker 2015). Some species do manage to persist and have established urban populations globally such as common kestrels (*Falco tinnunculus*), northern goshawks (*Accipiter gentilis*), sparrowhawks (*Accipiter nisus*) and the peregrine falcon (*Falco peregrinus*, hereafter peregrine) (Rutz 2008; Sumasgutner et al. 2014b; Thornton et al. 2017). For the peregrine, this follows their recovery from widespread population crashes due to pesticide use (Kauffman et al. 2003; Pagel et al. 2018), among other anthropogenic stressors (reviewed by Chace and Walsh 2006). Urban peregrines today may experience greater breeding success and chances of survival than their rural conspecifics, with this success typically attributed to suitable prey and nesting

sites in urban environments (Cade and Bird 1990; Kettel et al. 2018, 2019; Wilson et al. 2018; Mak et al. 2021). These *non-traditional habitats* can be of high quality for the species (Chace and Walsh 2006; Kettel et al. 2018, 2019; Wilson et al. 2018; Mak et al. 2021) and some urban centres already act as source areas for metapopulations (White et al. 2002; Sielicki and Sielicki 2009; Pagel et al. 2018). However, some populations may misinterpret environmental cues and breed in suboptimal urban locations and succumb to 'ecological traps' (Klein et al. 2007; Sumasgutner et al. 2014a).

Urban environments differ greatly from other locations that would traditionally provide peregrine habitats, but common features among these locations allow for habitat analogues (Lundholm and Richardson 2010). For example, tall buildings may be broadly similar to steep cliff faces and rock outcrops that provide natural peregrine nesting sites (Gainzarain et al. 2000; Jenkins and van Zyl 2005; Brambilla et al. 2006; Francis

2021), especially church towers that often provide nest sites for breeding raptors (Taylor 2003; Drewitt and Dixon 2008; Sumasgutner et al. 2014b). Urban environments also offer peregrines plenty of novel but attractive hunting opportunities, with prey congregating around features such as bird feeders and even artificial illumination (reviewed by Mak et al. 2021). Together, these factors may influence breeding peregrine site selection (Brambilla et al. 2006), assessing which urban resources are useful to raptor populations can provide a detailed understanding of their ecological requirements, which will facilitate the meeting of conservation objectives. This is typically done through tracking of animal movements in their habitat (Rutz 2006; Tanferna et al. 2013; Martínez-Miranzo et al. 2016; Apolloni et al. 2018) or by studying the habitat characteristics around known breeding sites (Jenkins 2000a; Gainzarain et al. 2000; Sumasgutner et al. 2014b). For peregrines, these types of studies have so far been limited to more natural sites, and few focus on breeding populations (Dobler 1993; Jenkins and Benn 1998; Gainzarain et al. 2000; Lapointe et al. 2013; Martínez-Welgan 2017). Furthermore, Martínez-Welgan (2017) noted a paucity of studies on peregrine spatial use at a finer scale than home range, which encompasses both the breeding and the larger foraging habitat (Johnson 1980; Bildstein and Therrien 2018).

Urban peregrine activity often attracts attention from interested members of the public, as the species is both charismatic and relatively uncommon, providing increasing opportunities for citizen science for obtaining information on local peregrine activity (Quinn 1995; Dickinson et al. 2010; Sumasgutner et al. 2014b). Furthermore, this form of data collection poses minimal risk and distress to wildlife (Götmark 1992; Schaefer 2004), a concern shared by members of the peregrine community across UK (pers obs). Therefore, in this study, we use locations of recorded peregrine sightings submitted by the public to an online conservation NGO database (managed by Greenspace Information for Greater London, or GiGL) to investigate which habitats are selected by urban peregrines breeding in London, relative to their availability within our study area.

Method

Study area

Our study area encompasses Greater London, UK (51.50° N, 0.12° W; C. 1600 km²; Fig. 1), a region of approximately 9 million inhabitants within the City of London and 32 administrative boroughs. London has abundant green space, with about 47% of its area covered by semi-natural habitat and public and private green spaces, 2% covered by water (e.g., rivers, canals) and the rest predominantly built development and infrastructure (GiGL CLC 2019; Fig. 1). Urban peregrines have been observed breeding in London since 1998 (Johnson 2014), nesting exclusively on human-made structures, some of which have nest boxes or substrate provided following occupation of the sites to furnish stable and secure nesting platforms (S. Harrington, personal communication).

Breeding site data

In this study, we define breeding site as the eyrie structure (e.g., building) on which peregrine eggs are laid (*sensu* Ratcliffe 1993). We retrieved 7502 peregrine sighting reports recorded between 2003 and 2018 from Greenspace Information for Greater London Community Interest Company (GiGL CIC), which consolidates records, from opportunistic sightings to systematic species

surveys, submitted by its partners and members of the public. All records included dates and location of each sighting, registered in Universal Transverse Mercator coordinates within 100 m precision. Of these, 4035 contained recorders' comments on their observations, which we reviewed to filter out non-breeding activity (e.g. hunting, perching, flyovers), leaving us with 56 sightings of breeding peregrines (e.g. references to eggs, feeding young or the terms 'breeding' and 'nest'). To contextualise these sightings, we plotted their coordinates over a Google Satellite map of Greater London using QGIS software v3.12. We omitted all spatially overlapping points and replaced points found within 100 m (consistent with the precision of our data-points) of each other with their geometric centroids. This was done to control for multiple submissions of the same sites in a year or across successive years, some of which were from different recorders who may each report a nest location with varying levels of accuracy. Additionally, none of the remaining points that were adjacent to each other were simultaneously reported in the same year, indicating specific nesting pairs may have shifted from nearby sites (i.e. different building in the same area), and we considered these as different breeding sites. We identified a total of 30 unique breeding sites (Fig. 1), 28 from following this process and 2 other sites we identified from another ongoing study. Using the nearest neighbour analysis function in QGIS v3.12, we also calculated the mean spacing between breeding sites [nearest neighbour distance (NND) 2155.3 m].

Habitat composition and analyses

To evaluate habitat composition, we overlaid the 30 breeding sites with a 10 m resolution raster CORINE land cover (CLC) 2018 map of Greater London which classified the available habitats into 20 CORINE categories (European Environment Agency 2017; Kosztra et al. 2019). We referenced this against the Ordnance Survey Open Greenspace map (Ordnance Survey 2020) to refine some of the green habitat categories and regrouped them into 11 new categories: allotment (land subdivided into smaller parcels used for non-commercial cultivation of usually non-arboreal fruits and vegetables), cemetery, agriculture, forested areas ('wood'), public parks or gardens ('park/garden'), recreational fields ('recreation'), water, infrastructure, quarries, dumpsites ('dump') and built-up areas ('built'; landcover dominated by urban structures such as buildings and roads and comprising 30–100% sealed soil) (Table 1; refer to Kosztra et al. 2019 for CLC classification nomenclature). We defined peregrine breeding habitat ('used') as the area within 500 m and 2000 m radii of each of the 30 breeding sites identified. These buffer distances were used in the absence of published data on the home range of urban nesting peregrines but follow similar methods used in other studies where tracking data is also unavailable (e.g. Sergio et al. 2005; Mathieu et al. 2006; Sumasgutner et al. 2014a,b; Jankowiak et al. 2015). We used 500 m buffers—a similar distance to Mathieu et al. (2006), Sumasgutner et al. (2014a,b) and Jankowiak et al. (2015)—as peregrine breeding territories may each contain (i) several potential eyries in which they nest and (ii) a number of perch sites from which they hunt (Ratcliffe 1993; Jenkins and Benn 1998; Jenkins 2000b; Brambilla et al. 2006). Therefore, this distance allows us to detect breeding habitat selection driven by such behaviour which may be overlooked at finer scales (e.g. fourth-order habitat selection (Johnson 1980) or 100 m buffers in Tanferna et al. 2013). Our use of 2000 m buffers was informed by the mean observed NND in our dataset (2155.3 m), similarly used by Sergio et al. (2005) and Sumasgutner et al. (2014a,b). We then generated 30 random points and created

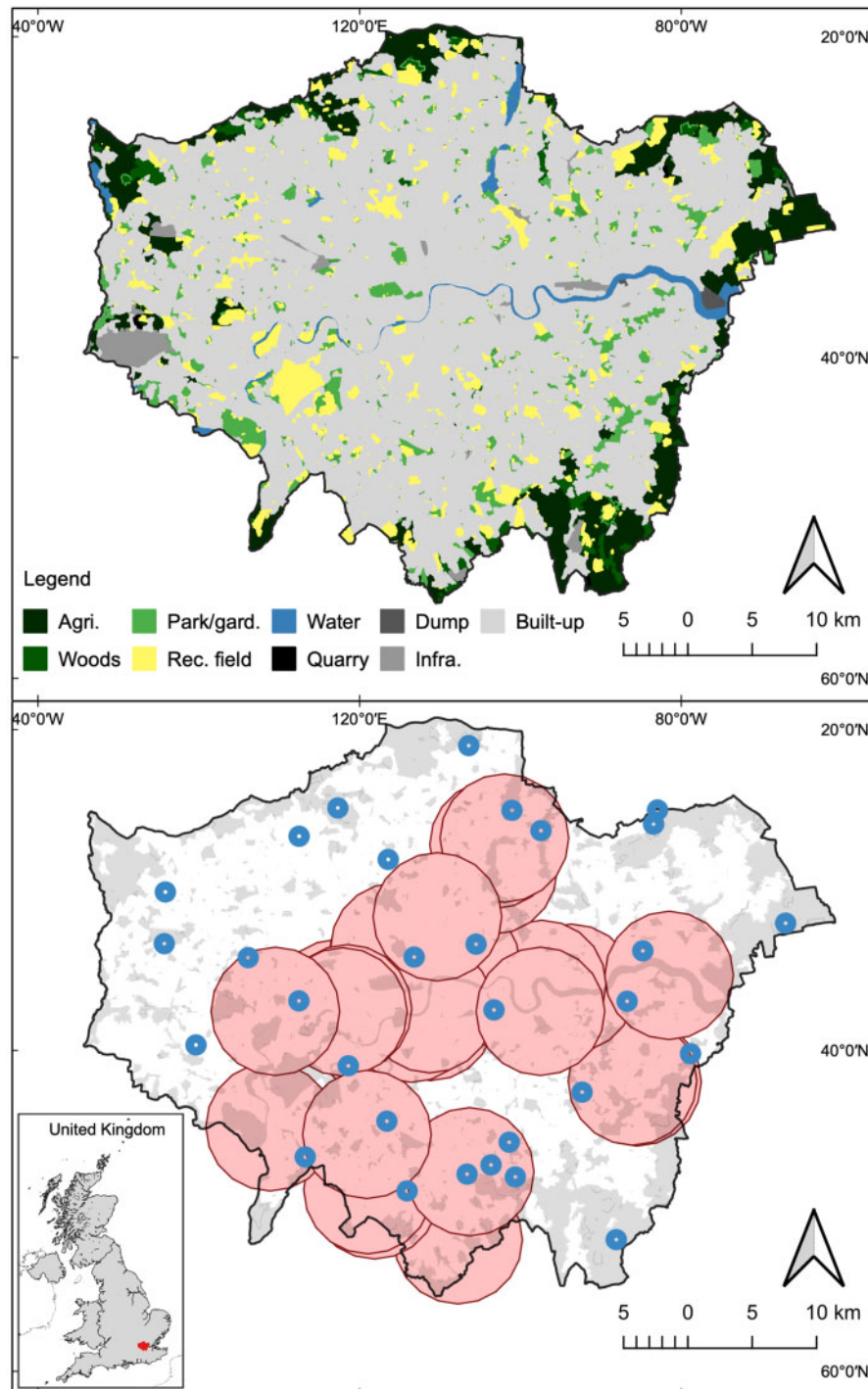


Figure 1: Nest sites of peregrines in London (51.50° N, 0.12° W) from 2003–2018 (within red circles, $n = 30$; presented at 10 km resolution to mask nest location in compliance with National Biodiversity Network publication guidelines on sensitive species) within our study area (c. 1600 km²) and random points (blue circles, $n = 30$). Allotments and cemeteries are illegible at this scale.

500 m and 2000 m buffers around each point to represent ‘available’ habitat for comparison. Within both groups (‘used’ and ‘available’), we calculated the proportion of each habitat category present at the two scales. We analysed breeding habitat selection at both scales to make our findings comparable with other studies.

We determined habitat preferences using compositional analysis (Aebischer et al. 1993), which transforms proportions of

habitat use and availability into their log-ratios, and allows for ranking of habitat types. This method encompasses Multivariate Analysis of Variance (MANOVA) analyses to determine whether habitat use significantly differs from random use based on habitat availability, in addition to 5000 iterations of randomisation tests we performed as recommended by Adams and Anthony (1996), from which we assessed the resultant Wilk’s Lambda, P and randomised P statistics. Compositional

Table 1: Habitat type present in our study area reclassified from habitat categories in CLC 2018 (European Environment Agency 2017) and OS Open Greenspace (Ordnance Survey 2020).

Habitat type	Original classification	
This study	CLC 2018	OS Open Greenspace
Allotment	–	Allotments/community growing space (land for non-commercial cultivation of fruits/vegetables)
Cemetery	–	Cemetery Religious grounds
Agriculture	Non-irrigated arable land Fruit trees and berry plantations Pastures Complex cultivation patterns Land principally occupied by agriculture	
Wood	Broad-leaved forest Coniferous forest Mixed forest Transitional woodland-shrub	–
Recreational field		Golf course Other Sports Play space Playing field Tennis court
Public park or garden	Green urban areas	Park Garden
Water	Inland marshes Intertidal marshes Water courses Water bodies Estuaries	
Infrastructure	Road and rail networks and associated land Port areas Airports	
Quarry	Quarry	
Dump	Dumpsite	
Built-up area	Continuous urban fabric (>80% covered with impermeable surfaces including buildings, roads, and artificially surfaced areas) Discontinuous urban fabric (30–80% covered with impermeable surfaces)	

Refer to Kosztra et al. (2019) for CLC classification nomenclature.

analyses also produce matrices of *t* values and differences of the log-ratios for habitat pairs, allowing for habitats to be ranked based on the significance of their differences. We replaced the values of non-utilised habitat with the value 0.001, an order of magnitude smaller than the lowest observed non-zero value, as suggested by Aebischer et al. (1993). We considered *P* significant at <0.05. Compositional analysis was performed using the *compans* function in *adehabitatHS* package (Calenge 2006), and all statistical analyses were performed in R v3.6 (Core Team 2013).

Results

Nearest neighbour analysis

The mean distance between nests in our study area was 2155.3 m (range: 314.5–7666.6 m), with a *z*-score of –2.53 indicating clustering of nests.

500 m buffer

Habitat composition found within 500 m of peregrine breeding sites was significantly different compared to our randomly selected locations ($\lambda = 0.360$, $P = 0.0002$, randomised $P = 0.0008$).

Of the nine habitat types found here, habitats categorised as water, public parks or gardens, built-up areas and cemeteries were used to a greater extent than they were available, indicating nesting preference for these habitats at this scale by breeding pairs (Table 2 and 3; Fig. 2). In contrast, infrastructure, recreational fields, agriculture and allotments were used to a lesser extent than they were available, while wooded areas were not used at all. Water was the most preferred habitat type, with significantly greater average log-ratios than most other alternatives, followed by public parks or gardens and then built-up areas (Table 2 and 3). However, the differences between log-ratios of the top three habitat categories (water, built-up areas, parks or gardens) were not significant. There were also no detectable differences between the log-ratios of cemeteries and infrastructure and these categories were tied at the fourth rank. Recreational fields, woodlands, agriculture and allotments were the least preferred habitat types.

2000 m buffer

Habitat composition found within 2000 m of peregrine breeding sites was significantly different from our randomly selected locations ($\lambda = 0.311$, $P = 0.001$, randomised $P = 0.0001$). Of the 11

Table 2: Results of the compositional analysis at 500-m scale, addressing breeding habitat preferences based on comparison of habitats used within the study area

Habitat	Water	Park/garden	Built	Cemetery	Infrastructure	Recreation	Wood	Agriculture	Allotment
Water	0	1.9593	2.0068	2.7404	3.3898	3.7184	3.7570	4.4166	5.1112
Park/garden	-1.9593	0	0.0474	0.7811	1.4303	1.7591	1.7977	2.4573	3.1519
Built	-2.0068	-0.0474	0	0.7337	1.3830	1.7117	1.7503	2.4099	3.1044
Cemetery	-2.7404	-0.7811	-0.7337	0	0.6493	0.9780	1.0167	1.6762	2.3708
Infrastructure	-3.3898	-1.4304	-1.3830	-0.6493	0	0.3287	0.3672	1.0269	1.7214
Recreation	-3.7184	-1.7591	-1.7117	-0.9780	-0.3287	0	0.0386	0.6982	1.3928
Woods	-3.7570	-1.7977	-1.7503	-1.0166	-0.3673	-0.0386	0	0.6596	1.3541
Agriculture	-4.4167	-2.4573	-2.4099	-1.6762	-1.0269	-0.6982	-0.6596	0	0.6945
Allotment	-5.1112	-3.1519	-3.1044	-2.3708	-1.7214	-1.3928	-1.3541	-0.6945	0

Proportions of habitat elements available at each individual nest were compared to that of random sites (see details in text). This table gives the mean differences in log-ratios for pairwise comparison between 'used' and 'available' habitat elements (in rows and columns, respectively). These were subject to pairwise t-tests. Positive values indicate greater use and negative values indicate lower use. Significant values at $P < 0.05$ in bold. The number of positive values ranks the order of use. Ranking of habitat preference (from most to least use; > denotes non-significant preference over subsequent category, = indicates tie): water > park/garden > built > cem = infra > rec > wood > agri > allot.

Table 3: t-values of pairwise significance tests between 'used' and 'available' habitat elements (in rows and columns, respectively) at 500-m scale

Habitat	Water	Park/garden	Built	Cemetery	Infrastructure	Recreation	Wood	Agriculture	Allotment
Water	0	1.8832	1.8232	2.2191	4.1309	3.2471	3.7619	4.6723	5.1966
Park/garden	-1.8833	0	0.0099	0.8589	1.5641	1.5361	2.1285	2.2874	3.3519
Built	-1.8232	-0.0099	0	1.2799	1.6876	1.7012	1.9388	2.1512	3.9212
Cemetery	-2.2191	-0.8589	-1.2799	0	0.5266	0.7405	1.0510	1.3832	3.1014
Infrastructure	-4.1309	-1.5641	-1.6876	-0.5266	0	0.1047	0.6615	1.3282	2.2882
Recreation	-3.2471	-1.5361	-1.7012	-0.7405	-0.1047	0	0.6456	0.9428	2.1317
Woods	-3.9077	-2.2268	-1.9464	-1.3174	-0.6142	-0.0742	0	1.0187	1.6896
Agriculture	-4.7677	-2.4382	-2.1490	-1.6732	-1.3707	-0.7272	-1.0187	0	0.8235
Allotment	-5.1296	-3.3753	-3.6824	-3.2795	-2.1693	-1.6891	-1.6895	-0.8235	0

habitat types covered, habitats categorised as water, public parks or gardens, built-up areas and infrastructure were also used to a greater extent than they were available, indicating nesting preference for these habitats by breeding pairs at this scale (Tables 4 and 5; Fig. 2). In contrast, allotments, cemeteries, recreational fields, agriculture and wooded areas were underutilised, while quarries and dump sites were not used at all. Water was the most preferred habitat type, with significantly greater average log-ratios than all other alternatives, followed by built-up areas and then public parks or gardens (Tables 4 and 5). However, the differences between log-ratios of public parks or gardens and built-up areas were not significant. There were also no detectable differences between the log-ratios of allotments and cemeteries and these categories were tied at the seventh rank. Allotments, cemeteries, recreational fields, woodlands and agriculture were the least preferred habitat types in this order.

Discussion

In this study, we have used public-sighting data to identify the breeding habitat preference of peregrines in London, which to our knowledge is the first study of its kind focusing on urban populations of the species. Even though this approach deviates from conventional telemetry-based studies and is limited in its ability to estimate the magnitude of use within each habitat category, our results suggest the relative order of habitat preference for nesting by peregrines (Quinn 1995). Compared to other studies of urban raptors (Rutz 2006; Tanferna et al. 2013;

Martínez-Miranzo et al. 2016; Apolloni et al. 2018), our use of citizen science has allowed for data to be collected over a larger space and time (Dickinson et al. 2010).

Our analyses have produced generally similar results at two different scales showing that water, public parks or gardens and built-up areas are most preferred habitat types among urban peregrines in our study. In contrast, all other forms of green space are less important to, or avoided by, urban breeding peregrines—recreational fields, wooded areas, allotments and agriculture are consistently the least preferred habitats at both scales. However, London's peregrine population density may also be approaching saturation with new arrivals driven to select less optimal sites (S. Harrington, personal communication). This is indicated by our high but significant Wilk's Lambda statistic ($\lambda = 0.360$ and 0.311) from compositional analysis and the close proximity at which they nest here (mean NND = 2.16 km; $z = -2.53$) compared to conspecifics in other regions, such as San Francisco Bay and Cape Peninsula where mean NND is 7.69 km and 3.13 km, respectively (Jenkins and van Zyl 2005; Venu 2018).

We have found that peregrines prefer built-up areas where tall buildings analogous to nesting cliffs used in natural settings are readily available (Gainzarain et al. 2000; Jenkins and van Zyl 2005; Brambilla et al. 2006; Rodríguez et al. 2007; Gahbauer et al. 2015). In London, peregrines colonise suitable ledges or nest boxes to lay their eggs similar to other building-nesting species (Taylor 2003; Drewitt and Dixon 2008; Johnson 2014; Sumasgutner et al. 2014b). The preference for water around breeding sites echoes that of other studies conducted in mostly natural settings (Brambilla et al. 2006; Rodríguez et al. 2007;

Lapointe et al. 2013; Gahbauer et al. 2015; Martinez-Welgan 2017; with exceptions in Wightman and Fuller 2005). This may be due to peregrines colonising the nearest suitable sites they could find while dispersing along river corridors from exurban or coastal areas (Kauffman et al. 2003; Dzialak et al. 2005;

Gahbauer et al. 2015). However, unlike built-up areas, waterbodies and public parks or gardens (the latter at 2000-m scale) *per se* are unlikely to contain suitable nesting features and yet the preference for these habitat types precede built-up areas. This may indicate that peregrines consider nest site suitability together with other opportunities (e.g. hunting) in the landscape when selecting breeding sites (Brambilla et al. 2006). Urban kestrels prefer nesting in buildings with green backyards where prey can be easily accessed (Sumasgutner et al. 2014b) and peregrines may similarly be selecting breeding sites where they can hunt, in addition to the dedicated foraging sites within their home range (Riegert et al. 2007; Bildstein and Therrien 2018). Peregrines are highly sedentary and prefer to perch hunt, thus the ability to forage around their nests allows them to conserve energy (Dobler 1993; Jenkins and Benn 1998; Lapointe et al. 2013).

In our study area, tall buildings line the green and blue spaces in the urban core, such as Regent’s Park and the River Thames, and peregrine selection of these suitable buildings located on the edges of densely built-up areas adjacent to hunting grounds matches observations of peregrine site selection during their early stages of colonising London (S. Harrington, personal communication). This combination of land cover types—of tall buildings typical to built-up areas juxtaposed with the adjacent low-lying spaces such as water and public parks or gardens—provides contrasting topographical relief similarly found at cliff sites which peregrines use to their advantage; the commanding view of the surrounding landscape not only allows peregrines to seek prey and detect threats while attending to the nest but also increase their hunting success when initiating hunts from greater heights (Skaggs et al. 1988; Dobler 1993; Ratcliffe 1993; Jenkins 2000a,b; Wightman and Fuller 2005; Dzialak et al. 2007; Time 2016). In the urban context, peregrines using nest sites located near the edges of natural spaces can intercept prey *en route* to or from these habitat patches that become exposed when crossing between buildings, which also conceal the peregrines from prey (Jenkins 2000a; Rutz 2006; Dzialak et al. 2007; Gahbauer et al. 2015). This may be why our visual inspection of locations reveals that the least preferred sites (recreational fields, woodlands, agricultural sites, allotments) are located beyond the urban centre where tall buildings are less likely dominate the landscape, providing peregrines fewer of such opportunities

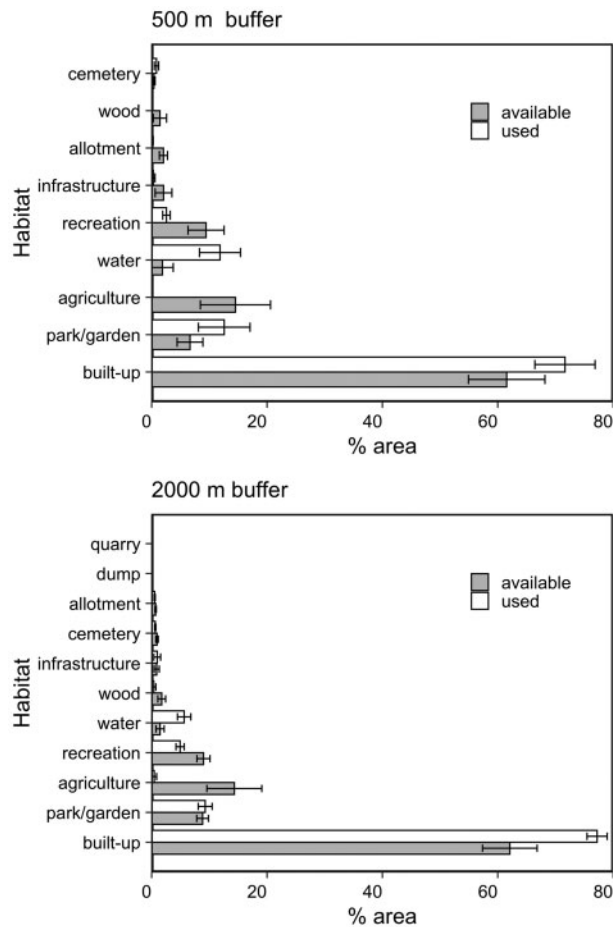


Figure 2: Mean percent area of the habitat elements present at used and available sites at 500 m and 2000 m scales. Error bars represent ±1 standard error.

Table 4: Results of the compositional analysis at 2000-m scale, addressing breeding habitat preferences based on comparison of habitats used within the study area

Habitat	Water	Built	Park/garden	Quarry	Infrastructure	Dump	Allotment	Cemetery	Recreation	Wood	Agriculture
Water	0	2.4754	2.6774	2.9284	2.9860	3.0888	3.2680	3.3445	3.5304	4.3713	5.5713
Built	-2.4754	0	0.2020	0.4530	0.5105	0.6133	0.7926	0.8691	1.0549	1.8958	3.0960
Park/garden	-2.6774	-0.2020	0	0.2510	0.3085	0.4113	0.5906	0.6671	0.8530	1.6939	2.8940
Quarry	-2.9284	-0.4530	-0.2510	0	0.0575	0.1603	0.3396	0.4161	0.6019	1.4430	2.6429
Infrastructure	-2.9860	-0.5105	-0.3085	-0.0575	0	0.1028	0.2821	0.3586	0.5444	1.3853	2.5854
Dump	-3.0888	-0.6133	-0.4113	-0.1603	0.1028	0	0.1793	0.2557	0.4416	1.2826	2.4826
Allotment	-3.2680	-0.7926	-0.5906	-0.3396	-0.2821	-0.1793	0	0.0765	0.2624	1.1033	2.3033
Cemetery	-3.3445	-0.8691	-0.6671	-0.4161	-0.3586	-0.2557	-0.0765	0	0.1859	1.0268	2.2268
Recreation	-3.5304	-1.0549	-0.8509	-0.6019	-0.5444	-0.4416	-0.2624	-0.1859	0	0.8410	2.0410
Wood	-4.3713	-1.8958	-1.6939	-1.4429	-1.3853	-1.8252	-1.1033	-1.0268	-0.8409	0	1.2001
Agriculture	-5.5713	-3.0959	-2.8940	-2.6429	-2.5854	-2.4826	-2.3033	-2.2268	-2.0410	-1.2001	0

Proportions of habitat elements available at each individual nest were compared to that of random sites (see details in text). This table gives the mean differences in log-ratios for pairwise comparison between ‘used’ and ‘available’ habitat elements (in rows and columns, respectively). These were subject to pairwise t-tests. Positive values indicate greater use and negative values indicate lower use. Significant values at $P < 0.05$ in bold. The number of positive values ranks the order of use. Ranking of habitat preference (from most to least use; >> denotes significant preference over subsequent category, > denotes non-significant preference over subsequent category): water >> built > park/garden > quarry > infra > dump > allot = cem > rec > wood > agri.

Table 5: t-values of pairwise significance tests between 'used' and 'available' habitat elements (in rows and columns, respectively) at 2000-m scale

Habitat	Water	Built	Park/garden	Quarry	Infrastructure	Dump	Allotment	Cemetery	Recreation	Wood	Agriculture
Water	0	3.0844	3.0356	3.6535	3.5449	4.0937	3.7891	4.0583	4.1863	3.7788	4.4787
Built	-3.0844	0	0.7230	2.5522	0.9391	2.6974	2.3391	2.8740	3.7328	2.6592	3.6276
Park/garden	-3.0356	-0.7230	0	0.7499	0.5084	1.1056	1.3283	1.5417	2.4576	2.0400	3.2629
Quarry	-3.6535	-2.5522	-0.7499	0	-0.1063	1.0000	0.8272	1.3299	2.5262	2.2955	3.6893
Infrastructure	-3.5449	-0.9391	-0.5084	-0.1063	0	0.2012	0.3968	0.4949	0.8405	1.5180	2.6775
Dump	-4.0937	-2.6974	-1.1056	-1.0000	-0.2012	0	0.3955	0.7312	1.3611	1.9407	3.1725
Allotment	-3.7894	-2.3390	-1.3283	-0.8272	-0.3968	-0.3955	0	0.1980	0.7394	1.3211	2.5148
Cemetery	-4.0583	-2.8741	-1.5417	-1.3299	-0.4949	-0.7312	-0.1980	0	0.5417	1.4894	2.5129
Recreation	-4.1863	-3.3728	-2.4576	-2.5262	-0.8405	-1.3611	-0.7394	-0.5417	0	1.2941	2.7417
Wood	-3.7788	-2.6592	-2.0400	-2.2955	-1.5178	-1.9407	-1.3211	-1.4894	-1.2941	0	1.7192
Agriculture	-4.4787	-3.6276	-3.2629	-3.6893	-2.6775	-3.1725	-2.5148	-2.5129	-2.7417	-1.7192	0

even if there is an adequate prey base (Jenkins and Benn 1998; Lapointe et al. 2013; Martinez-Welgan 2017).

The aversion to open habitat (recreational fields, agricultural sites) in our analyses departs from observations of rural peregrine populations (Lapointe et al. 2013; Martinez-Welgan 2017) while that of closed habitat (woodlands) has been similarly recorded elsewhere (Jenkins 2000a). This avoidance may stem from a combination of the lack of preferred topographical relief around or within these locations capable of supporting their sedentary hunting style; these habitats are located away from the urban core and prey therein may not be as abundant (particularly synurbic species such as feral pigeons); or the vegetation structure offers insufficient cover and they are thus avoided by potential prey, while dense vegetation cover makes prey too difficult to capture (Jenkins 2000a; Dzialak et al. 2007). Therefore, parks and gardens with their mosaic of patchy vegetation are analogous to the moderate and uneven canopies peregrines in more natural settings favour for hunting, as they can opportunistically take vulnerable prey moving between cover (Jenkins 2000a; Dzialak et al. 2007).

Management implications

Appreciation for green and blue spaces in cities is growing due to their value for human and nonhuman users; further attention should be given not only to these habitats but also to their surroundings on account of their importance for breeding peregrines as well as other urban birds of prey (Dobler 1993; Rutz 2006; Fröhlich and Ciach 2018). Additionally, we need to consider how combinations of contrasting habitat types such as built-up areas with waterbodies or parks and gardens provide favourable topographical relief for species traditionally using cliff habitats (which buildings in urban environments are analogous to) and their surroundings (Wightman and Fuller 2005; Jenkins 2000b; Brambilla et al. 2006).

As urbanisation reduces and fragments semi-natural habitats (McDonald et al. 2009), and taller buildings replace older developments, their use by building-nesting raptors should be anticipated and we recommend that provisions be made to accommodate them, as long as the habitat is ecologically suitable and people tolerant of their presence (Johnson 2014; Mak et al. 2021). If not, raptor colonisation should be discouraged to avoid ecological traps or conflict (Klein et al. 2007; Sumasgutner et al. 2014b). Additionally, within such areas likely to be used, surveys for peregrine presence during or close to the breeding season should be proactively conducted prior to any potentially

disturbance-inducing human activities such as building maintenance being carried out, to avoid deleterious effects or conflict where possible. This is especially crucial in cities where peregrine populations are still growing, given the role urban environments play in the recovery of peregrine populations globally (Pagel et al. 2018; Kettel et al. 2018). Planners should also be aware of the discriminatory use of greenspaces by raptors as reported here when designing urban spaces intended to balance conservation goals and human recreational needs (Mak et al. 2021). However, more studies tracking spatial use by urban peregrines are needed to understand the extent of their home range in these environments as well as how intensively each habitat type is used (e.g. Rutz 2006; Martinez-Welgan 2017), as our dataset only allows for analyses of core breeding habitat preferences rather than that of their broader foraging range. Furthermore, we have assumed that habitats present around the nest are used or intentionally selected for by peregrines.

Our use of public sighting data circumvents logistical and welfare concerns associated with handling wildlife in the process of tagging them for research (e.g. Rutz 2004; Lövy and Riegert 2013, personal observation), but is prone to spatial bias (Götmark 1992; Quinn 1995). Additionally, the presence of peregrines at sites with less human activity may go under-reported but having consulted with peregrine groups, we are confident our public-sighting dataset encapsulates a representative sample of the urban peregrine population in Greater London given how the highly charismatic raptors draw lots of attention which increases the likelihood of their recording.

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Conflict of interest statement

The authors declare that they have no competing interests.

Authors' contributions

B.M., R.F., and M.C. conceived the research; B.M. collected and analysed the data; and B.M., R.F., and M.C. wrote the paper. All authors contributed critically to the drafts and gave final approval for publication.

Data availability

GIS habitat and nearest neighbour distance data used for our analyses will be available from the King's Research Data Management System. Peregrine location data have been used under license from GiGL and requests should be made directly to GiGL due to sensitivity of data.

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