

The Impacts of Humans And Dogs On The Spatial And Temporal Activity of Wildlife In Urban Woodlands

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Research Article

Keywords: urban ecology, camera traps, woodland species, human disturbance, temporal activity, spatial activity

Posted Date: February 2nd, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-854180/v1>

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Version of Record: A version of this preprint was published at Urban Ecosystems on August 24th, 2023. See the published version at <https://doi.org/10.1007/s11252-023-01414-z>.

Abstract

Humans can derive enormous benefit from the natural environment and the wildlife they see there, but increasing human use may negatively impact wildlife, particularly in urban green spaces. Few studies have focused on the trade-offs between intensive human use and wildlife use of shared green spaces in urban areas. In this paper we investigate the impacts of humans and their dogs on wildlife within an urban green space using camera trap data from Hampstead Heath, London. Spatial and temporal activity of common woodland wildlife species were compared between sites with low and high frequency of visits by humans and dogs. Blackbirds (*Turdus merula*) were found to be significantly more active at sites with lower visitation rates, while red foxes (*Vulpes vulpes*) were observed more in areas with higher visitation rates. Birds and grey squirrels (*Sciurus carolinensis*) showed evidence of temporal displacement away from peak periods of human and dog visits in areas where visitation rates were high. Responses observed to human and dog visits could have implications for wildlife species persistence and community composition in urban woodlands.

Introduction

Enjoyment of green spaces in urban areas is important to mental health and wellbeing, and a key aspect of this effect is the interaction with nature and wildlife (Soulsbury and White, 2015; Triguero-Mas et al, 2015). However, there is growing evidence that recreational use of public green spaces can be a form of human disturbance affecting the abundance, diversity and behaviour of wild species (Larson et al, 2016; Gaynor et al, 2018). Negative effects of human disturbance may be stronger in urban green spaces than in more rural landscapes as resources are more limited and there is less space and time to avoid humans (Gaynor et al, 2018). Understanding how wildlife is impacted by human disturbance in urban green spaces will allow us to develop solutions that minimise negative impacts. This will benefit both wildlife and humans who will potentially have a greater variety and abundance of wildlife species to enjoy (Soulsbury and White, 2015; Triguero-Mas et al, 2015).

Use of urban green spaces like Hampstead Heath is growing as people value time spent outside and in nature. For instance, estimated visits to Hampstead Heath rose from 7 million to 9.3 million between 2007 and 2018 (Intelligent Space ATKINS, 2007, p. 75; City of London, 2019), while the 2020 pandemic appears to have increased visits by 50% in a single year (City of London, unpublished). When surveyed in 2017, visitors to the Heath reported enjoyment of nature as the most common reason for their visits (Groundwork London, 2017).

This study examines how the behaviour of wildlife on Hampstead Heath is affected by recreational visits by humans and dogs (*Canis familiaris*). It is focused on woodland bird and mammal species that forage on the ground, including nocturnal species that have some activity in the morning and evening. Woodlands on our study site, Hampstead Heath, are criss-crossed by a network of walking paths used by visitors. A large proportion of visitors also bring dogs to Hampstead Heath, usually off-leash, which is typical across green spaces in England (Taylor et al, 2005). Few studies on wildlife activity include the effect of visitors accompanied by dogs, but those that do show that dogs, like humans, can further affect wildlife activity (Fernández-Juricic and Tellería, 2000; Dowding et al, 2010; Banks and Bryant 2007; Reilly et al, 2017). As dogs, even those off-leash, are found in close association with humans, we combined the visits of humans and dogs and analysed how wildlife species responded to the overall presence of both species. We hypothesised that wildlife species would be observed less in areas of woodland with high frequency of human and dog visits, and would shift their temporal activity patterns in those areas to avoid this form of disturbance. We expected this effect to be stronger for diurnal than nocturnal species.

We tested whether visiting humans and dogs affect the behaviour of wildlife species using camera traps. Camera traps provide a unique opportunity to understand small scale patterns in temporal and spatial overlap and interactions across species within vertebrate communities (Rowcliffe and Carbone, 2008) and are increasingly used at a range of scales from local communities to global-scale meta-analyses (Steenweg et al, 2016). For this study, we utilised images from a 2018 camera trap survey set up to study hedgehogs by the London HogWatch Project (Carbone and Cates, 2018). This survey captured activity of species foraging on woodlands based on a systematic grid-based camera survey (see Rowcliffe et al, 2014). By recording continuous photographic data across multiple independently selected woodland sites, we were able to obtain unbiased spatial and temporal information on wildlife occurrence and activity in areas that differed in levels of human and dog visitation.

Methods

Study Area

Hampstead Heath is a 275-hectare urban green space, which is listed as a site of Metropolitan Importance for Nature Conservation and situated in a densely populated part of Central London (City of London, 2019). Hampstead Heath comprises a mosaic of habitats including woodland, grassland, scrub and open water, which are managed to maintain a diverse and biodiverse landscape while ensuring access by visitors (City of London, 2010; City of London, 2019). Wildlife surveys show woodlands, including an ancient woodland designated as a Site of Special Scientific Interest (Natural England 1990), to be particularly rich in breeding bird and mammal species (City of London, unpublished).

Data Collection

Between 18th April and 5th July 2018, camera traps were uniformly distributed over Hampstead Heath across 150 sites using a 150 m² cell-size

grid overlay (Monterroso et al, 2013). Each camera trap operated on average for 15 days (range: 9 - 23 days) and recorded continuously 24 hours a day. Survey lengths varied due to limited storage on memory cards, batteries running out of charge and camera failures. Camera traps were attached 20-50 cm above the ground to suitable features nearest to the ideal coordinates, for example fence posts or trees. Traps were angled slightly downwards to increase the probability of recording wildlife. Traps minimised disturbance by passively detecting wildlife using heat signatures (Welbourne et al, 2016) and were not baited. 104 camera traps across four models were used: 64 Browning Strike Force HD-Pro BTC-131 5HDPs, 20 Reconyx HyperFire HC-500s, 10 Reconyx Hyperfire HC-600s and 10 Reconyx Hyperfire PC-800s. The Browning model took one image per trigger with a delay of approximately 0.6 seconds between photos, while the Reconyx models took ten images per trigger with a delay of one second (specifications for these cameras can be found at www.trailcampro.com).

Camera Site Selection

For the purpose of this study, a subset of 26 camera traps were selected from woodland sites across Hampstead Heath (Online Resource-Table 1). Camera traps were selected in woodland designated as “at least 84% broadleaved woodland”, with the exception of one camera in a wooded copse in “semi-neutral improved grassland” (City of London, 2009; Online Resource-Table 2). Broadleaved woodland sites were dominated by English oak (*Quercus robur*) and less frequently by common beech (*Fagus sylvatica*) and sessile oak (*Quercus petraea*), with an understory of bramble (*Rubus fruticosus*), holly (*Ilex aquifolium*) and other small trees, and a ground cover of common ivy (*Hedera helix*) or bracken (*Pteridium aquilinum*) (See Online Resource-Table 2 for full habitat descriptions by site). Within this habitat, all camera traps were positioned to give a clear view of open leaf litter to five metres with little ground cover under a closed canopy. This improved the detection probability for all wildlife species, especially hedgehogs which can go undetected in tall vegetation (Sollmann et al, 2013). Importantly, the distribution of cameras across the Heath meant some were close to, and others distant from, foot paths. Some were in the few fenced off woodland areas on the Heath, which people and dogs rarely visited. This created a broad range in frequency of human and dog visits recorded between traps.

Photo Review

All vertebrate species within camera images were manually identified using ExifPro v2.1 (Kowalski, 2013) and classed as ‘detections’ and/or ‘contacts’. When an animal enters a camera’s field of view, the camera triggers and takes a series of successive images of the animal. Each successive image of that animal was classed as a ‘detection’, while the first image, indicating the arrival of a new individual, was classed as a ‘contact’. Hence a contact was often the first image in a series of detections for an individual of a particular species. While the sum of all detections from a specific trap gives a measure of the total time spent by that species at that site, the sum of contacts estimates the total number of individuals of that species visiting the site. To estimate contacts, we assumed that an interval of two or more minutes between successive detections of a species represents the arrival of a new individual (Kay and Parson, 2014). For wildlife species, humans and dogs, we recorded total contacts as an indicator of visits to a particular site. Dogs on and off leads were both counted as contacts.

Wildlife Selection

Across the 26 camera traps, images of 18 distinct species of wildlife were captured, with some species being particularly common (Table 1). Diurnal species included a range of ground-foraging birds and grey squirrels (*Sciurus carolinensis*), while nocturnal species included mostly red foxes (*Vulpes vulpes*) and European hedgehogs (*Erinaceus europaeus*). For our analysis of wildlife activity, we put species in groups (All Birds and Non-diurnal Mammals) and also investigated individual species where we had enough detections.

Table 1 Summary of wildlife species detected in camera images across the 26 sites, with the number of absolute and relative detections (out of total 13,617 wildlife detections), and the number of sites at which the species was detected in camera images.

Common Species Name	Latin Name	Total Number of Detections	Proportion of Wildlife Detections	Total Sites
Common Blackbird	<i>Turdus merula</i>	1,646	12%	19
Magpie	<i>Pica pica</i>	999	7%	21
Song Thrush	<i>Turdus philomelos</i>	478	4%	13
Wood Pigeon	<i>Columba palumbus</i>	956	7%	12
Other Birds ^a	-	501	4%	18
European Hedgehog	<i>Erinaceus europaeus</i>	482	4%	18
Grey Squirrel	<i>Sciurus carolinensis</i>	6,402	47%	26
Red Fox	<i>Vulpes vulpes</i>	1,769	13%	24
Other Mammals ^b	-	386	3%	10

Table 1 footnotes: ^a 'Other birds' consists of blue tits (*Cyanistes caeruleus*), carrion crows (*Corvus corone*), dunnocks (*Prunella modularis*), Eurasian jays (*Garrulus glandarius*), great tits (*Parus major*), European robins (*Erithacus rubecula*) and wrens (*Troglodytes troglodytes*), which individually have very few tags and often were present at only a few sites.

^b 'Other mammals' consists of brown rats (*Rattus norvegicus*), wood mice (*Apodemus spp.*), European rabbits (*Oryctolagus cuniculus*) and muntjacs (*Muntiacus reevesi*), which individually have very few tags and were present at only a few sites.

More frequently observed species were also better represented over a range of sites with different levels of humans and dog visits. Based on total detections, we selected four bird species for individual analysis: common blackbirds (*Turdus merula*), magpies (*Pica pica*), song thrushes (*Turdus philomelos*), and wood pigeons (*Columba palumbus*). We also created for analysis the category "All Birds" in order to incorporate these species and the individually rare but collectively significant diversity of "Other Birds" (Table 1). Three species of mammals were analysed individually: red foxes, grey squirrels and European hedgehogs. Because mammal species were, broadly speaking, either diurnal, crepuscular or nocturnal, and likely respond to differently to daytime visits by humans and dogs (Gaynor et al, 2018), we created for analysis a group of "Non-diurnal Mammals" comprising red foxes, European hedgehogs, wood mice (*Apodemus sylvaticus*), European rabbits (*Oryctolagus cuniculus*) and muntjac (*Muntiacus reevesi*). Grey squirrels were the only diurnal mammal species analysed. Camera trap records of brown rats showed them to be predominantly diurnal (Online Resource-Figure 1b), but their numbers were so few that they were excluded from the analysis.

Statistics

Establishing sites of low and high human and dog visits

Human and dog contacts, separately recorded at each site, were summed and divided by the time of operation of the camera at each site to generate Relative Abundance Indices (RAIs) in contacts per day (Carbone et al, 2001). We justify the use of these "Human + Dog RAIs" on the basis that dogs were not seen without humans, and the effects of both on wildlife could not be easily separated. Human and dog visits were highly correlated (simple linear regression with logged RAIs: $b=0.67$, $p\text{-value}<0.01$, $R^2=0.70$; Online Resource-Table 3 and Figure 2).

Human + Dog RAIs per site ranged from zero for cameras in remote, fenced areas to 127 contacts day⁻¹ for cameras near busy paths. Examining all sites, we identified a natural breakpoint between four and eight human and dogs contacts per day (Reilly et al, 2017; Online Resource-Figure 3). Sites with less than five humans and dogs contacts per day were defined as low visit sites ($n = 17$, median = 2 contacts day⁻¹), while sites with five or more human and dogs contacts per day were defined as high visit sites ($n = 9$, median = 13 contacts day⁻¹).

Spatial Displacement

To determine potential spatial displacement, RAIs were also calculated for wildlife species at each site. Wildlife RAIs were put into low and high visit site groups and the two groups compared using Wilcoxon tests, due to the general non-homogeneity of variances, lack of normality and unequal group sizes.

Temporal Displacement

To examine temporal displacement of wildlife by human and dog visits, we calculated at each site the degree of temporal overlap between Human + Dog detections and the detections for different wildlife species, and then compared these results between our low and high visit sites. We assumed that at low visit sites, where human and dog disturbance is less, the observed activity schedules are more likely to reflect the natural times of activity for a species. Hence, reduced temporal overlap at high visit sites would mean that species are being displaced from their natural activity schedules (Reilly et al, 2017).

To calculate temporal displacement, detections were used, rather than contacts, as the method requires total species activity and does not need to distinguish individuals (Rowcliffe et al, 2014). Camera models differed in photographic rate, meaning that they generated different numbers of detections in response to a species crossing in front of the camera. By filtering the data so that only detections recorded at least one minute apart were included in the analysis, these camera differences were removed (note: measuring spatial displacement did not require correcting for camera differences as it utilised contacts, which are at least two minutes apart).

Timestamps were then converted to sunTime to standardise how sunrise and sunset varied between 18th April and 11th June across the 26 sites: times at sunrise and sunset were standardised to $\pi/2$ and $3\pi/2$ respectively. This corrected for changes in timings of behaviour due to the seasonal photoperiod change (Nouvellet et al, 2012; Meredith and Ridout, 2020).

Temporal overlap estimates were generated using the R package 'Overlap' (Ridout and Linkie, 2009; Meredith and Ridout, 2020). 'Overlap' converts sunTime, in radians, into non-parametric kernel density estimates for each species, i.e. activity schedules (Ridout and Linkie, 2009; Meredith and Ridout, 2020). The activity schedule across 24 hours of each species is then superimposed with that generated for combined

humans and dogs. The area underneath where the two activity schedules overlap is the temporal overlap estimate, which has a value between 0 and 1 that represents no and complete temporal overlap respectively (Ridout and Linkie, 2009; Meredith and Ridout, 2020).

To be selected for individual analysis, a species needed to have at least ten detections to produce robust estimates of temporal activity (Díaz-Ruiz et al, 2016). If either species (i.e. a wildlife species or humans + dogs) in the temporal overlap analysis had less than 75 detections, density estimates were generated using the Dhat1 estimator with a smoothing coefficient of 0.8 (Meredith and Ridout 2020). This estimator compensates for the reduced number of detections by over smoothing the activity schedule to increase its overall accuracy (Ridout and Linkie, 2009). Alternatively, the Dhat4 estimator was used which has a smoothing coefficient of 1. To estimate the accuracy of the temporal overlap estimates, we generated 95% confidence intervals by recalculating the temporal overlap estimates 1,000 times using bootstrapping (Meredith and Ridout, 2020).

Finally, temporal overlap estimates between each wildlife species and humans and dogs were compared between low and high visit sites using Wald Chi-Squared tests. The formula for which is as follows:

$$Wald \chi^2 = \frac{(T_H - T_L)^2}{(se_H - se_L)^2}$$

where T_H and T_L are the temporal overlap estimates from high and low visit sites, respectively, and se_H and se_L are the standard errors of these estimates from high and low visit sites, respectively. Using a degree of freedom of one, temporal overlap estimates from low and high visit sites were statistically significant if the chi-squared value was greater than 3.841 (p -value < 0.05).

All plotting and analyses were conducted in R v.3.6.2 (R Core Team, 2019).

Results

Across 26 sites, the total trapping effort was 389 days. In total, 13,617 wildlife detections of 18 species (Table 1), and 18,156 detections of humans and dogs were recorded, with 10,897 human detections and 7,259 dog detections. In low visit sites, the median and mean Human + Dog RAI were 1.52 contacts day⁻¹ (95% CI[0.22, 2.81]) and 1.47 contacts day⁻¹, respectively, while in high activity sites they were 13.23 contacts day⁻¹ (95% CI[8.83, 126.57]) and 28.14 contacts day⁻¹ respectively.

Spatial Displacement

Results are shown in Table 2. Blackbirds had significantly lower RAIs in high visit sites than in low visit sites, while all bird species combined (All Birds) and other individual species did not show a significant difference. For mammals, red foxes had significantly higher RAIs in high visit sites, while European hedgehogs and grey squirrels showed no significant differences. Non-diurnal Mammals also showed increased RAIs at high visit sites, although this difference was not statistically significant and strongly influenced by fox detections.

Table 2 Median (Mean) Relative Abundance Indices of each wildlife species in low and high visit sites, and results from Wilcoxon tests comparing RAIs between low and high visit sites. Significant if p -value < 0.05 (in bold). Confidence intervals shown for medians only as data is not normally distributed.

Species	Median RAIs [95% CI] (low visits; contacts day ⁻¹)	Mean RAIs (low visits; contacts day ⁻¹)	Median RAIs [95% CI] (high visits; contacts day ⁻¹)	Mean RAIs (high visits; contacts day ⁻¹)	W statistic	p value
All Birds	1.36 [0.64, 4.18]	2.29	0.80 [0.11, 5.63]	1.46	49	0.15
Blackbird	0.58 [0.12, 3.42]	1.07	0.00 [0.00, 5.07]	0.12	27	<0.01
Magpie	0.15 [0.06, 0.58]	0.28	0.29 [0.00, 5.07]	0.98	83	0.75
Song Thrush	0.08 [0.00, 0.43]	0.32	0.00 [0.00, 0.86]	0.12	59	0.33
Wood Pigeon	0.00 [0.00, 0.17]	0.22	0.11 [0.00, 0.47]	0.14	98.5	0.21
Non-diurnal Mammals	1.02 [0.40, 1.72]	0.96	1.36 [0.96, 3.52]	1.74	113	0.05
European Hedgehog	0.14 [0.00, 0.37]	0.18	0.14 [0.00, 0.99]	0.21	73.5	0.89
Grey Squirrel	1.62 [0.72, 3.70]	2.58	1.52 [0.45, 4.66]	1.72	63	0.49
Red Fox	0.36 [0.07, 1.02]	0.51	1.13 [0.60, 3.52]	1.50	129	<0.01

Temporal Displacement

Fig. 1 Activity schedules showing the temporal overlap between Human + Dogs (blue solid) and a) All Birds, b) Blackbirds, c) Magpies, d) Song Thrushes, e) Wood Pigeons, f) Non-diurnal Mammals, g) Red Foxes, h) European Hedgehogs and i) Grey Squirrels (red dashed) in low visit sites (left column) and high visit sites (right column). For number of detections for each species, see Online Resource-Table 4. Figures made in R v3.6.2 (R Core Team, 2019)

Figure 1 shows the activity schedule of wildlife species at low and high visit sites. Note that the temporal distribution of Human + Dog detections varies between these categories, probably because dog walkers tend to use morning hours more than people walking on their own or in groups. Statistical analysis is shown in Table 3 (see also Online Resource-Table 4). All bird species combined (All Birds) showed significant temporal displacement at high visit sites with 22% less temporal overlap with humans and dogs than in low visit sites. Individually, blackbirds, wood pigeons and grey squirrels were significantly temporally displaced with 22%, 18% and 26% less temporal overlap at high visit sites, respectively. Magpies, song thrushes, red foxes, European hedgehogs and Non-diurnal Mammals showed no significant temporal displacement (Table 3, Figure 1, and Online Resource-Table 4)

Table 3 Summary of results from temporal displacement analysis: Temporal overlap estimates between humans and dogs and each wildlife species by low and high visit sites. Temporal overlap estimates range between 0 (no overlap) and 1 (complete overlap). Wald statistics from comparison of temporal overlap between human and dog visit sites and each wildlife species or group. Significant p-values (<0.05) in bold.

Species	Temporal Overlap-Low Visit [95% CI]	Temporal Overlap-High Visit [95% CI]	Wald Statistic	p-value
All Birds	0.93 [0.88, 0.96]	0.73 [0.67, 0.79]	32.13	<0.001
Blackbird	0.92 [0.87, 0.97]	0.72 [0.57, 0.86]	7.02	0.01
Magpie	0.76 [0.65, 0.86]	0.68 [0.60, 0.76]	1.48	0.22
Song Thrush	0.75 [0.65, 0.85]	0.72 [0.54, 0.85]	0.12	0.73
Wood Pigeon	0.89 [0.81, 0.96]	0.73 [0.55, 0.88]	4.08	0.04
Non-diurnal Mammals	0.10 [0.06, 0.14]	0.08 [0.05, 0.10]	0.12	0.73
European Hedgehog	0.07 [0.02, 0.12]	0.06 [0.01, 0.12]	0.04	0.84
Grey Squirrel	0.85 [0.80, 0.91]	0.63 [0.58, 0.69]	29.96	<0.01
Red Fox	0.12 [0.08, 0.17]	0.08 [0.05, 0.10]	2.27	0.13

Discussion

Our study examined the patterns of spatial and temporal displacement in birds and mammals in sites with low and high human and dog visits. As predicted, we found that diurnal wildlife showed greater tendency for spatial and temporal displacement in response to diurnal human and

dog visits compared to nocturnal species. Our results indicate that not all species were impacted uniformly. Table 4 summarises patterns of spatial and temporal displacement across all species and species groups.

Table 4 Summary of trends observed in spatial and temporal overlap. For spatial overlap, mean RAIs for high visit sites for each group and species (Table 2) are marked as reduced (-), increased (+) or unchanged (=) relative to low visit sites where differences in means exceed 20%. The same criteria are applied to temporal overlap estimates (Table 3). Significant differences at $p < 0.05$ (*) and $p < 0.01$ (**) are shown.

Species	Spatial overlap	Temporal overlap
All Birds	(-)	(-)**
Blackbird	(-) **	(-) **
Magpie	(-)	(-)
Song Thrush	(-)	(-)
Wood Pigeon	(+)	(-) *
Grey Squirrel	(-)	(-) **
Non-diurnal Mammals	(+)	(-)
European Hedgehog	(=)	(=)
Red Fox	(+) **	(-)

Many factors determine the activity of wildlife species in woodlands, including the local distribution of vegetation, food and water resources, and the location of burrows and nest sites. We measured one factor, the effects of visits by humans and dogs, and sought to control for other factors by selecting traps located in a specific vegetation type and microhabitat. Studies on the ecology of species observed corroborate their natural association with broadleaved woodland floors and their habit of foraging in leaf litter. This is an important microhabitat for blackbirds and song thrush (Carpenter et al, 2009), and one which is frequently used for foraging by wood pigeon (Robinson, 2005) and magpie (Birkhead, 2010). Broadleaved woodland floors are also used for foraging by squirrels (Gurnell, 1987; Kenward et al, 1998), foxes (Sidorovich et al, 2006) and hedgehogs (Riber, 2006). We focus our discussion on abundant wildlife species which were observed at more than half of all sites, making it more likely that differences seen related to human and dog visitation rather than other factors.

Blackbirds showed significant spatial and temporal displacement from high visit sites: less individuals were recorded in high visit sites and those that were recorded shifted their activity patterns to early morning, when human and dog visits were less frequent. Spatial displacement was not found for other bird species, but significant temporal displacement was found for the group 'All Birds', where detections of all bird species were pooled, and for wood pigeons. Generally, in low visit sites, all bird species showed a roughly midday peak in activity on the woodland floor, with the exception of song thrushes which exhibited a morning and evening activity peak. At high visit sites, the daytime peaks for all bird species were retained but diminished, and a separate, distinctive early morning activity peak appeared.

Magpies were the only bird species which showed a trend towards being more common in high visit sites, although the difference was not significant. Like some other corvids, this species is known to be anthropophilic (Gutzwiller et al, 2002; Larson et al, 2016), which may be related to their tendency to scavenge human food (Jerzak, 2001; Storch and Leidenberger, 2003) and to exploit the disruption of other birds by humans to find and predate on their nests (Groom, 1993; Gutzwiller et al, 2002; Marzluff and Neatherlin, 2006).

Our results for blackbirds are similar to those found by Fernández-Juricic and Tellería (2000) in city parks in Madrid. Using behavioural observation methods, they found that parks with more human and dog visits had fewer foraging blackbirds and that blackbirds were less frequently present at times of the day when visitors peaked (Fernández-Juricic and Tellería, 2000). The more common species in this study, including blackbirds, magpie and wood pigeons, were also less abundant in sections of parks with greater human disturbance (Fernández-Juricic, 2000). van der Zande and Vos (1984) also found evidence that recreational visits decreased local activity of blackbirds, song thrushes and wood pigeons in a wooded lakeside habitat in the Netherlands.

The only strictly diurnal mammal included in our study, grey squirrel, showed no spatial displacement at high visit sites but strong temporal displacement. Like birds, squirrels had a broad, daytime activity peak in low visit sites, but at high visit sites, this changed to two distinctive peaks before and after the main period of human and dog activity. As far as we are aware, our study provides the first evidence of how humans and dogs affect the temporal activity of grey squirrels.

Non-diurnal Mammals showed no spatial or temporal displacement in areas of high human and dog visits. In fact, foxes made significantly more visits to these areas, which probably accounted as well for the trend in Non-diurnal Mammals. Other studies have shown a positive spatial association between humans and foxes (Prange et al, 2004; Kays and Parsons, 2014; Oberosler et al, 2017; Reilly et al, 2017), which may reflect

attraction to food left by humans or greater abundance of natural foods, such as invertebrates and earthworms, created by path disturbance (Harris, 1981; Contesse et al, 2004). This study suggests that normal, diurnal recreation by humans with dogs does not displace hedgehogs, even in high visit areas. By contrast, a study on hedgehog activity associated with more intensive and nocturnal human activity at a music festival, demonstrated spatial and temporal displacement (Rast et al, 2019).

By displacing wildlife species in space or time, human disturbance on Hampstead Heath could be impacting the ability of the affected species to forage effectively, and hence reducing their reproductive success (Ditchkoff et al, 2006; Diaz-Ruiz et al, 2016; Larson et al, 2016; Gaynor et al, 2018). There is evidence that recreational use of trails in natural woodlands decreases both bird activity and breeding (van der Zande and Vos 1984; Bötsch et al. 2017, Bötsch et al. 2018). While our study only found significant displacement for quite common species like blackbirds and squirrels, similar displacement of less common species may have more impact on their survival and persistence. On Hampstead Heath, for instance, song thrush and mistle thrush (*Turdus viscivorus*) are nationally declining species (Burns et al, 2020) that forage in the same woodland floor habitat as blackbirds, but nesting bird surveys in 2020 and 2021 show that they are considerably less common (City of London, unpublished). They were not well captured in this study, but more focused camera trapping might determine how they are affected by human and dog visits.

Camera traps have a history of being used to study rare, widely ranging mammals in remote areas, but have seldom been used in urban green spaces and to study birds and common urban mammals. This study shows their potential value to the study of small-scale spatiotemporal patterns of habitat use in response to disturbance, at both the individual species and community level. Using camera traps overcomes the problems of more typical focal observations, including any bias from the presence of a human observer and the limited time period for such observations. This results in more accurate observations of wildlife activity and increases the likelihood of capturing long term changes to it. However, our study does have other limitations which need highlighting.

Most importantly, other factors may have influenced wildlife activity besides disturbance by humans and their dogs. While we could not correct for potentially confounding factors, we sought to reduce their impact by selecting woodland sites with very similar plant composition and microhabitats, and by focusing on common and widespread species. Secondly, Hampstead Heath is not a typical urban green space as it exhibits both high ecological diversity and intense recreational use, which may limit the general applicability of our findings. Finally, in measuring wildlife responses against the combined presence of humans and dogs, we were unable to examine their potentially different effects. For instance, dog walking was more frequent in the morning (Online Resource-Figure 2) when we also saw the most striking temporal displacement of birds and squirrels, implying dogs may have a disproportionate impact on wildlife.

In conclusion, our study provides evidence that the spatial and temporal activity of some woodland species in urban green spaces is changed as a result of recreational visits by human and their dogs. Further research should focus on the implications of this disturbance for local wildlife populations and their reproductive success, particularly for more vulnerable species, and on the separate effects of humans and dogs, in order to identify specific approaches to reducing impacts from recreational visits in urban green spaces on biodiversity.

Declarations

Funding

The data collection using camera traps was majorly funded by the British Hedgehog Preservation Society, the People's Trust for Endangered Species, and the Pauline Meredith Charitable Trust. CC was funded by Research England.

Conflicts of Interest

The authors have no conflicts of interest to declare.

Availability of Data and Material

The original images and resulting dataset are not publicly available to protect the privacy of those recorded.

Code Availability

All code is currently available by request from the corresponding author.

Author's Contributions

Jeff Waage, Chris Carbone and Rachael Beasley contributed to the study conception and design. Data collection was performed by Chris Carbone and Adrian Brooker. Analysis was performed by Jeff Waage and Rachael Beasley. The first draft of the manuscript was written by Rachael Beasley and Jeff Waage. All authors commented and edited previous versions of the manuscript. All authors read and approved the final manuscript.

Ethics Approval/Consent to Participate/Consent for Publication

Signs were placed around Hampstead Heath informing visitors that camera traps were in use. No effort was or will be made to identify visitors recorded by the camera traps.

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Figures

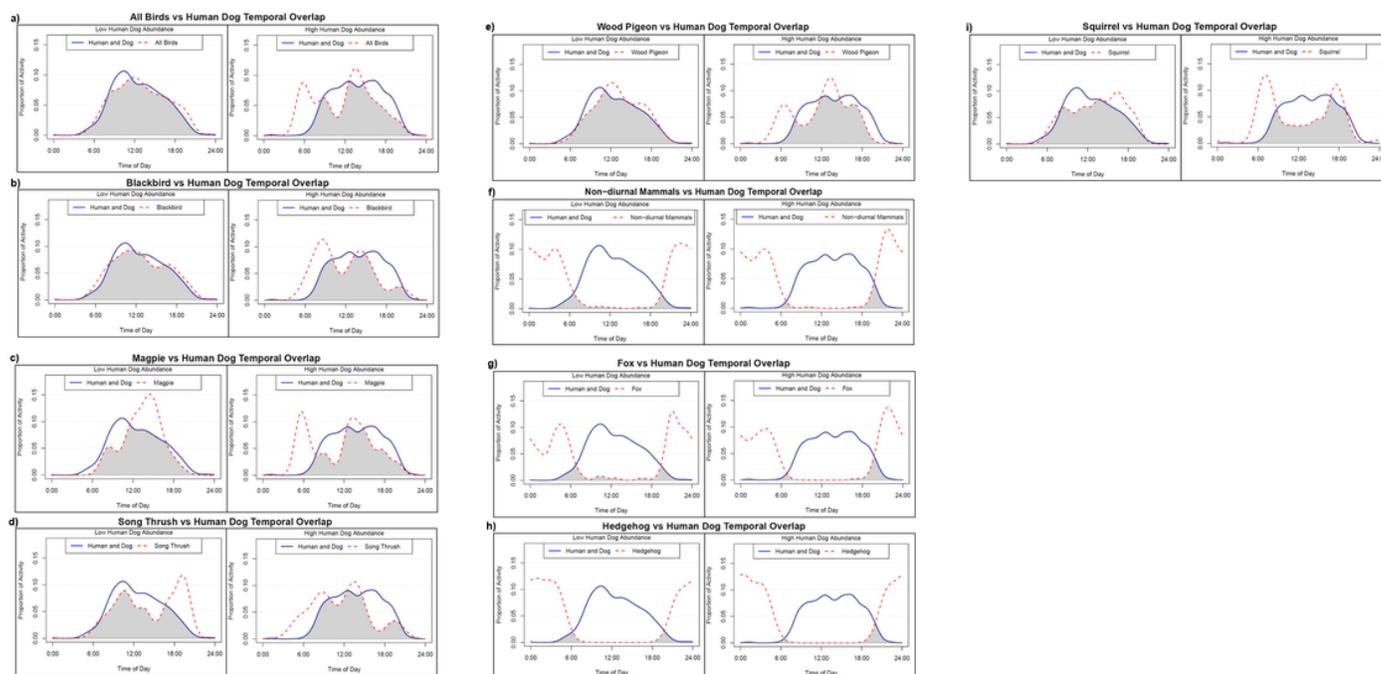


Figure 1

Activity schedules showing the temporal overlap between Human + Dogs (blue solid) and a) All Birds, b) Blackbirds, c) Magpies, d) Song Thrushes, e) Wood Pigeons, f) Non-diurnal Mammals, g) Red Foxes, h) European Hedgehogs and i) Grey Squirrels (red dashed) in low visit sites (left column) and high visit sites (right column). For number of detections for each species, see Online Resource-Table 4. Figures made in R v3.6.2 (R Core Team, 2019)

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