Global Ecology and Conservation 51 (2024) e02873

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Effects of human disturbance on detectability of non-breeding birds in urban green areas

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ARTICLE INFO

Keywords:
Detection probability
Urban dwellers
Non-breeding season
Phenology
Weather conditions
Urban parks

ABSTRACT

Animals adapted to disturbed habitats have evolved multiple behavioural strategies, spanning from hiding to displacing to less disturbed microhabitats. Urban areas pose new evolutionary challenges since animals often need to deal with novel environmental conditions. In this context, urban parks may constitute biodiversity hotspots within the concrete jungle. Nonetheless, the recent increase in recreational activities in urban parks potentially puzzles the ability of urban-dwelling animals to exploit these environments. In this study, we evaluated the effect of human disturbance and other contextual variables on the activity patterns of four bird species commonly found in European urban parks, covering a wide range of ecological characteristics: the blackbird (*Turdus merula*), the hooded crow (*Corvus cornix*), the Eurasian robin (*Erithacus rubecula*), and the wood pigeon (*Columba palumbus*). We performed repeated counts of these bird species in six urban parks in northern Italy and we fitted Bayesian N-mixture models to estimate the relationship between detection probability and human disturbance (number of people present in the park), phenology (date and time of the day), and weather conditions (temperature and precipitation). For all the species but the blackbird, we found a negative relationship between the number of people present in the park and the detection probability of the focal species. We also found species-specific effects of both phenology and weather conditions on the detection probability. Our results suggest that urban dwelling species can finely modulate their activity patterns in response to the level of human disturbance, suggesting a possible key role of behavioural phenotypic plasticity. Furthermore, uncovering patterns of detectability of urban fauna can help in planning biodiversity monitoring and conservation, as it provides useful information to carry out surveys when the probability of detecting individuals is highest, optimising resource investments and reliability of biodiversity estimates.

1. Introduction

Human disturbance has far-reaching effects on animals, globally restructuring both habitats and communities (Shochat et al., 2006), as well as altering individual behavioural responses (Beale and Monaghan, 2004). This is especially true for urban areas, where animals can face challenging conditions impacting activity patterns (Slabbekoorn and Peet, 2003), fitness (Chamberlain et al., 2009)

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https://doi.org/10.1016/j.gecco.2024.e02873
Received 10 November 2023; Received in revised form 6 February 2024; Accepted 28 February 2024
Available online 1 March 2024

and, ultimately, evolution (Johnson and Munshi-South, 2017). As a consequence, animals need to overcome such challenges by displacing in less disturbed areas or by behaviourally adapting to this high disturbance (Hahs et al., 2023; Tuomainen and Candolin, 2011; Zhou et al., 2020). Indeed, individuals may be forced to exploit microhabitats in more secluded areas within cities, thus spatiotemporally segregating from humans, e.g., by altering activity patterns (Fernández-Juricic and Tellería, 2000), or shifting to a more nocturnal lifestyle (Gaynor et al., 2018).

Some species, the so-called urban dwellers, are particularly tolerant towards human disturbance and can even reach strikingly higher densities in urbanised areas as compared to rural ones (e.g. tree sparrows in Denmark, 105 times denser in cities; Møller et al., 2012, but see Kurucz et al., 2021). These species generally show a higher behavioural plasticity (Capilla-Lasheras et al., 2022; Caspi et al., 2022; Lowry et al., 2013; Sol et al., 2013). Within these species, individuals in urban contexts are often more behaviourally plastic than those in rural areas. For instance, behavioural experiments showed that urban populations of the house sparrow (*Passer domesticus*) exhibit faster habituation rates compared to rural populations of the same species (Vincze et al., 2016). Additionally, urban house sparrows were larger and faster learners compared to rural ones in complex problem-solving tasks related to foraging (Papp et al., 2015). A similar pattern can also be witnessed by the variation in flight initiation distance, i.e., the distance at which individuals flee when approached by a person. In fact, in more urbanised areas, where the people density is higher, the fleeing distance of birds can be lower, likely as a plastic and/or adaptive response to constant disturbance in these environments (Mikula, 2014).

In urban landscapes, many species are concentrated in green areas, especially urban parks, which are thus acting as biodiversity hotspots in cityscapes (Korányi et al., 2021; Nielsen et al., 2014; Vasquez and Wood, 2022). This is particularly true for birds, which are known to prefer tree refuges over artificial ones (Morelli et al., 2022). Furthermore, urban parks provide welfare and life-quality services to citizens (Chiesura, 2004; Nghiem et al., 2021; Nutsford et al., 2013). However, human disturbance can potentially affect populations of animals living in green urban areas, with cascade effects on human well-being itself (Aronson et al., 2014).

A first sign of the negative effect of human disturbance may be witnessed by the spatial or temporal segregation of animal species from humans. Whenever animals segregate from humans, detection probability, i.e., the probability of seeing an individual during a survey, may be influenced. For instance, a lower human disturbance may result in a higher detection probability, with individuals being more visible when fewer people are present. Such a pattern has been neatly shown during the COVID-19 pandemic when, following the lockdown policies adopted by many countries, animals were more easily detected (Gordo et al., 2021; Manenti et al., 2020b). In fact, when fewer people are present, animals may be able to exploit areas that are normally above their fear tolerance threshold (Gordo et al., 2021).

Apart from human disturbance, additional factors may concur in influencing detection probability of animals in urban landscapes

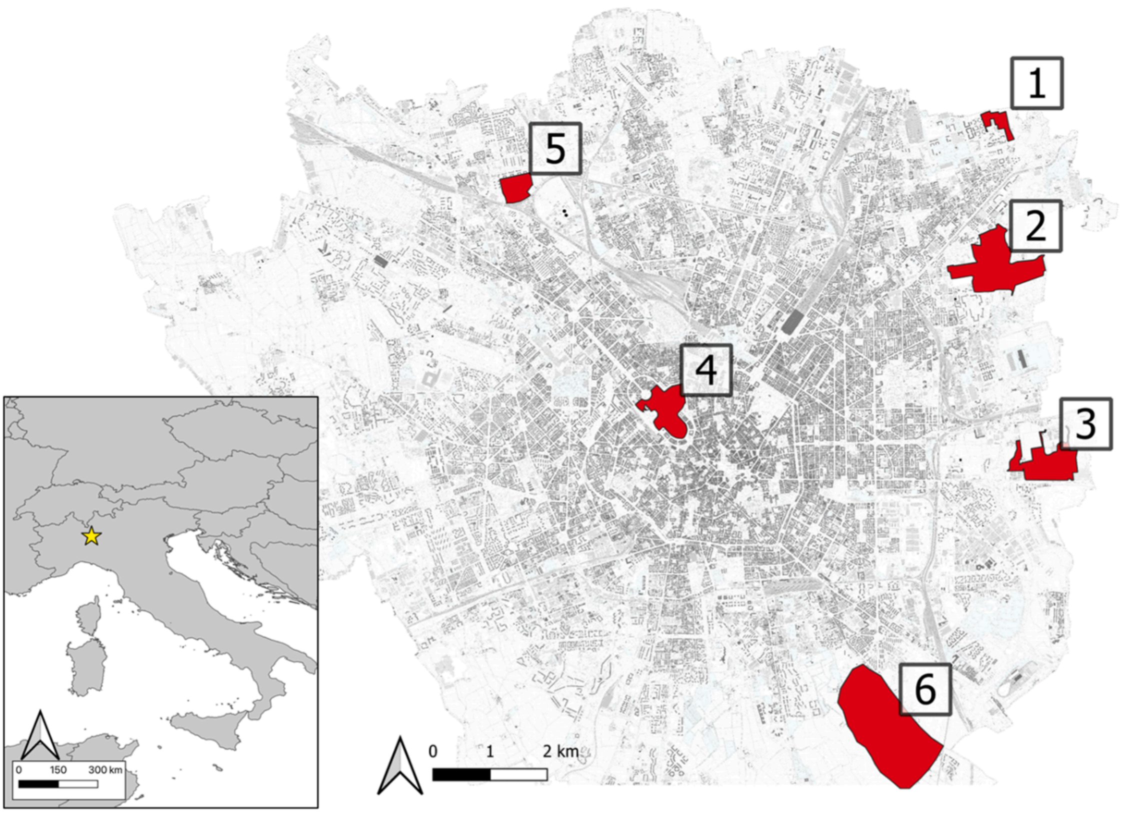

Fig. 1. Study area and surveyed urban parks. Study area (city of Milan) highlighted in red, the six surveyed urban parks: 1) Adriano, 2) Lambro, 3) Enrico Forlanini, 4) Sempione, 5) Franco Verga, 6) Vettabbia. The location of the city of Milan is shown in the bottom left panel.

(e.g., Vanek et al., 2019). Indeed, species' phenology and weather conditions can exert a strong influence on detection probability and, consequently, on survey counts and abundance estimates. For instance, migration arrival date can influence detection probability in birds (Strebel et al., 2014), while temperature and precipitation are well-known parameters strictly related to animal's activity (Dalpasso et al., 2023; Falaschi, 2021; Zuckerberg et al., 2011). Therefore, such potentially confounding effects need to be considered when analysing how human disturbance influences animals' detection probability.

Taking into account such confounding effects on birds' detection probability is particularly important, especially during the non-breeding season, which in temperate environments corresponds to the winter. In this period, the activity of seasonal breeders is unrelated to reproduction, as individuals are not tightly bound to the nesting site; therefore, the survival component of the fitness may be more important (Robinson et al., 2020; Shoji et al., 2015). Under these less favourable environmental conditions, seasonal breeders are likely to modulate their activity based on other factors that may influence their survival, such as weather conditions and human disturbance. In this respect, analysing the factors related to detection probability in the non-breeding season may prove crucial in planning monitoring activities, to carry out surveys when the probability of detecting the target species is highest. This is true also for the most common species, whose monitoring programs need to be carefully planned, since maximising the detection probability would ultimately provide more reliable and robust estimates of population size.

In this study, we evaluated the effect of human disturbance and other contextual variables on the activity patterns of four bird species commonly found in European urban parks: the blackbird (*Turdus merula*), the hooded crow (*Corvus cornix*), the Eurasian robin (*Erithacus rubecula*), and the wood pigeon (*Columba palumbus*). These are among the most common, widely distributed and abundant species that can be found in the Palearctic (Keller et al., 2020) as well as Italian (Lardelli et al., 2022) urban areas. Furthermore, these four study species belong to different guilds, spanning from generalists to insectivore specialists, from small- to medium/large-bodied species, from forest-dwelling to adapted to open habitats, as well as from small-scale migratory to resident species. Such a broad variety of life-history traits makes this set of species particularly suitable to represent the main guilds of birds in urban environments. Here, we performed repeated counts of these bird species in urban parks in Northern Italy during the non-breeding season. Then, we estimated the relationship between detection probability and human disturbance, phenology, and weather conditions. To our knowledge, no study has analysed these relationships, particularly during the non-breeding season. The underlying expectation was that at increasing levels of human disturbance, detection probability would decrease.

2. Materials and methods

2.1. Field surveys

We conducted 68 surveys in six urban parks in the city of Milan (Northern Italy: 45° 46' N; 9° 20' E; Fig. 1; see Table 1 for more details on the parks), the largest city of Northern Italy (> 1 million inhabitants; population density ~7500/km^2). In each park, we performed repeated surveys of 1 km transects with a 50 m sideband (i.e., 10 ha). Each transect was repeated 9–12 times in the period between November 2021 and February 2022, i.e., during the non-breeding season of our target species. Each transect path was walked at a slow speed (between 1 and 4 km/h) to count the individuals of the four target species (blackbird, hooded crow, robin, and wood pigeon). The transects were always surveyed in the same direction by a single observer. While walking along the survey transect, we counted all the individuals seen and heard, excluding flying-over individuals (i.e., those not interacting with the terrestrial biocenosis) as they might not be affected by ground-level conditions recorded by the observers (both human disturbance and weather conditions). As parks had a semi-open vegetation structure and most plants were leafless, visibility in the 50 m sideband was optimal.

Consecutive surveys were separated by at least seven days, resulting in a survey every 10.66 ± 4.37 (SD) days in each park. Surveys were planned to occur on different days of the week (i.e., no more than 2 surveys for each day of the week within a park), to avoid overrepresenting some days (e.g., weekends). Moreover, we conducted a maximum of four surveys per park in each one of the three time windows (~0–3, ~3–6, ~6–9 h after sunrise), to ensure a comparable representation of different times during the day.

2.2. Human disturbance, weather, and phenological variables

To assess the effect of human disturbance on birds detection probability, we considered the total number of people: we included both static and moving people, as well as bikers, but we did not include data on vehicles, contrary to other studies (Gómez-Serrano, 2021), as these are only rarely allowed in the studied parks, and likely have a negligible effect. The number of people was assessed by

Table 1
Summary information of the surveyed urban parks.

Park	Area (ha)	Blackbirds	Hooded crows	Robins	Wood pigeons	Number of people
Adriano	12.6	6.8 ± 3.5	5.9 ± 6.4	2.7 ± 1.1	3.6 ± 4.9	20.8 ± 9.1
Lambro	95.5	5.6 ± 2.6	22.7 ± 17.4	8.1 ± 4.3	5.8 ± 5.8	26.8 ± 18.5
Enrico Forlanini	55.7	4.4 ± 2.6	6.0 ± 2.2	4.0 ± 2.6	2.5 ± 2.5	32.6 ± 24.9
Sempione	46.3	10.6 ± 6.7	8.9 ± 6.5	5.0 ± 4.0	0.5 ± 1.5	207.6 ± 258.3
Franco Verga	21.5	4.6 ± 3.7	5.9 ± 3.6	2.7 ± 1.8	0.2 ± 0.6	52.9 ± 39.1
Vettabbia	203.7	3.7 ± 1.9	3.2 ± 2.6	3.8 ± 2.7	0.8 ± 1.4	17.7 ± 14.2

Summary information of the surveyed parks in Milan (Northern Italy). The mean (± SD) number of the focal species and the number of people (static, moving people and bikers) recorded during the surveys is reported.

the observer within the surveyed area (i.e., in the 10 ha buffer around the transect), contextually to the bird surveys.

Detection probability may also be affected by environmental conditions, such as weather, or by species-specific phenology, that may mask the effect of human disturbance. Hence, we included the time of the day (expressed as the absolute difference in minutes from midday) and the date (expressed as days after 1st November), to account for phenology. Furthermore, we included temperature and precipitation as weather variables. Temperature and precipitation were obtained from a publicly available database provided by the regional agency for the protection of the environment (downloaded from https://www.arpalombardia.it/temi-ambientali/meteo-e-clima/form-richiesta-dati/; accessed on 09/03/2022). We used 2 different meteorological stations and associated our survey data to the nearest meteorological station available in the regional database (Lambrate: 45.496781°N, 9.257516°E or Brera: 45.471658°N, 9.189111°E). Weather data had a temporal resolution of 10 min. We included the average temperature recorded during the survey (hereafter temperature) and the cumulative precipitation of the 24 h preceding the survey (hereafter precipitation).

2.3. Statistical analyses

We estimated the effect of human disturbance, weather, and phenological variables on the detection probabilities of the four study species, using N-mixture models. These are hierarchical models that are considered a robust and reliable method to estimate abundance and detection probability of birds (Royle, 2004) as well as other small vertebrates (Ficetola et al., 2018) as they allow to take into account the imperfect detection of the target species. In these hierarchical models, the true abundance (*N*) is treated as a latent variable and is jointly estimated by two submodels distinctively describing ecological and observational processes. One model describes the relationships between true abundance and ecological characteristics of the study sites (ecological model) and the second model describes the detection probability of individuals and its relationship with survey-specific covariates (observational model). In our analyses, true abundance was defined in the ecological model as following a Poisson distribution. In the observational model, individual

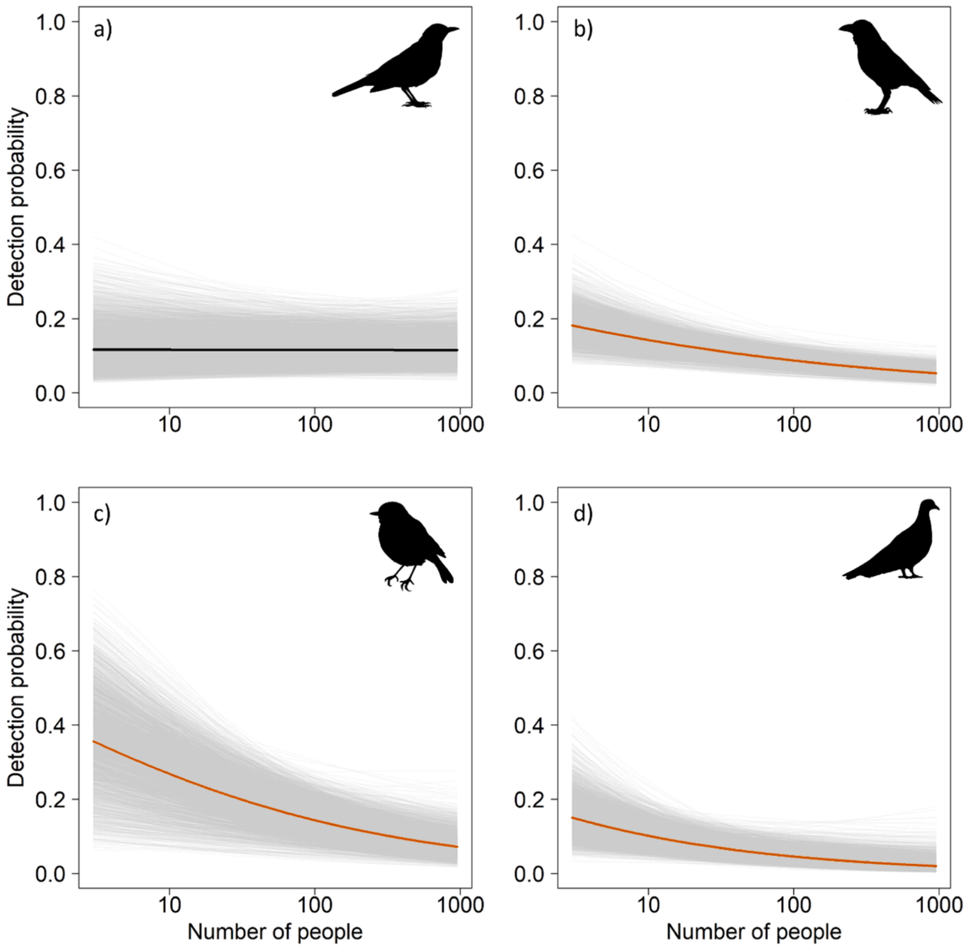

Fig. 2. Predicted relationships between detection probability and number of people. Marginal response curves for the effect of the number of people observed during the survey on the detection probability of individuals of a) blackbird, b) hooded crow, c) robin and d) wood pigeon. Thick lines represent the average predicted relationships, with orange curves depicting parameters for which credible intervals did not overlap zero. Grey lines represent 3000 samples from the posterior distribution (1000 for each chain).

counts in each site i and survey j ($y_{i,j}$) were described by a binomial distribution with sample size N_i and detection probability $p_{i,j}$:

$$y_{i,j} \sim Binomial(N_i, p_{i,j})$$

Detection probability was then related to a set of covariates: number of people (i.e., human disturbance), precipitation and temperature (i.e., weather), time of the day and date (i.e., phenology), as follows:

$$logit(E(p_{i,j})) = \alpha + \beta_{People} \times People_{i,j} + \beta_{Time} \times Time_{i,j} + \beta_{Date} \times Date_{i,j} + \beta_{Pcp} \times Pcp_{i,j} + \beta_{Tmp} \times Tmp_{i,j}$$

here, α is the intercept, β are the regression coefficients, and $People_{i,j}$, $Time_{i,j}$, $Date_{i,j}$, $Pcp_{i,j}$, and $Tmp_{i,j}$ are values of independent variables related to detection probability at site i and survey j. Before running the models, we $\log_{10}$-transformed the number of people and precipitation to reduce skewness. Furthermore, all variables were also standardised (subtracting the mean and dividing for the standard deviation) to improve convergence and allow the comparison of effect sizes. Correlation among independent variables was assessed with Pearson's pairwise correlation and was always weak ($|r| < 0.46$; Fig. S1), hence, we kept all the variables in the models.

Priors of regression coefficients of detection parameters followed a normal distribution with mean = 0 and precision = 0.01. For each species, we run 3 Markov Chains Monte Carlo for 40,000 iterations per chain, discarding the first 30,000 as a burn-in. We sampled the distribution of posteriors with a thinning of 10, resulting in 1000 posteriors for each chain. Finally, we evaluated the convergence of parameters both visually and by looking at the R_{hat} values as previously done in other studies (Jiménez-Franco et al., 2019; Manenti

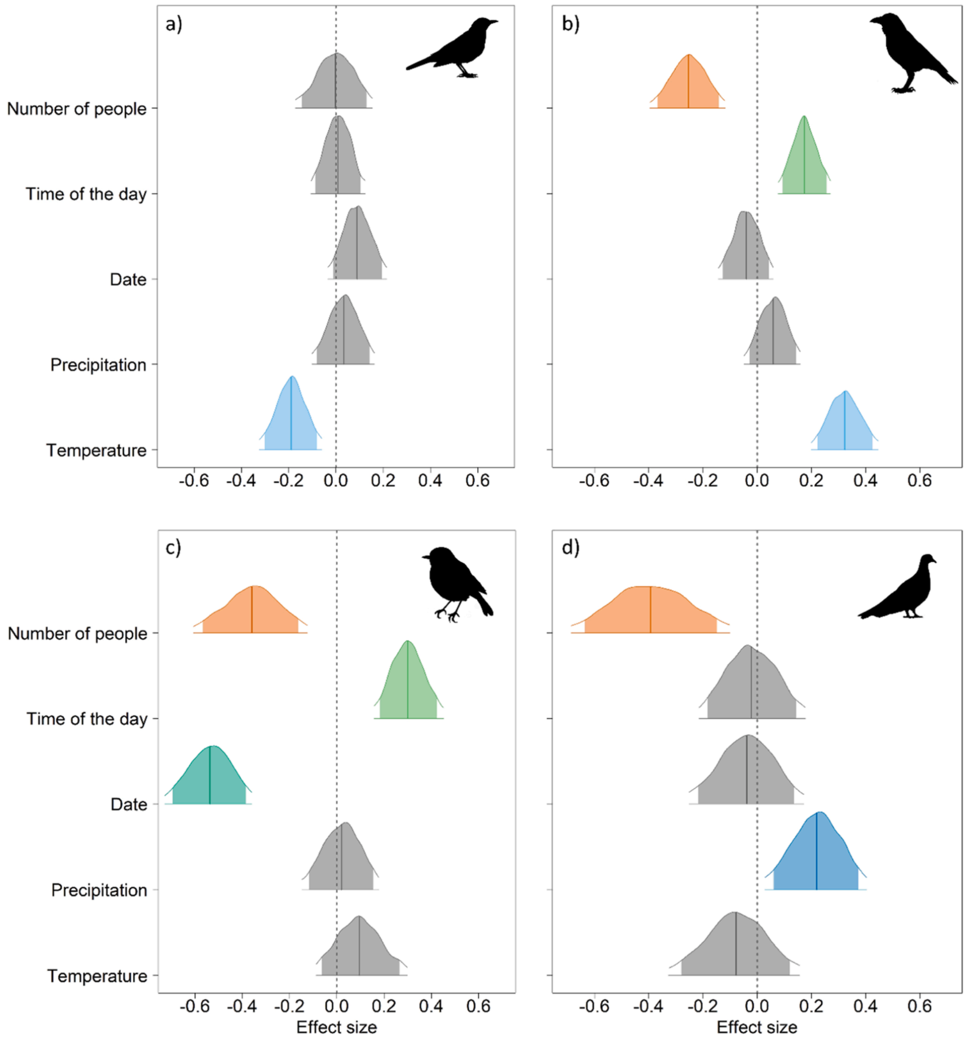

Fig. 3. Density plots of the posterior distribution of the effect of variables related to detection probability. Each panel represent the parameters estimated by models of each species: a) blackbird, b) hooded crow, c) robin and d) wood pigeon. The posterior distribution is shown for human disturbance (orange), phenology (green) and weather (blue) variables. Posterior distributions for which the 95% credible intervals (CIs) overlapped 0 are shown in grey. Thick vertical lines represent the average estimated effect for each variable. The curve lines represent the 95% credible intervals, while the shaded areas represent the 90% credible intervals.

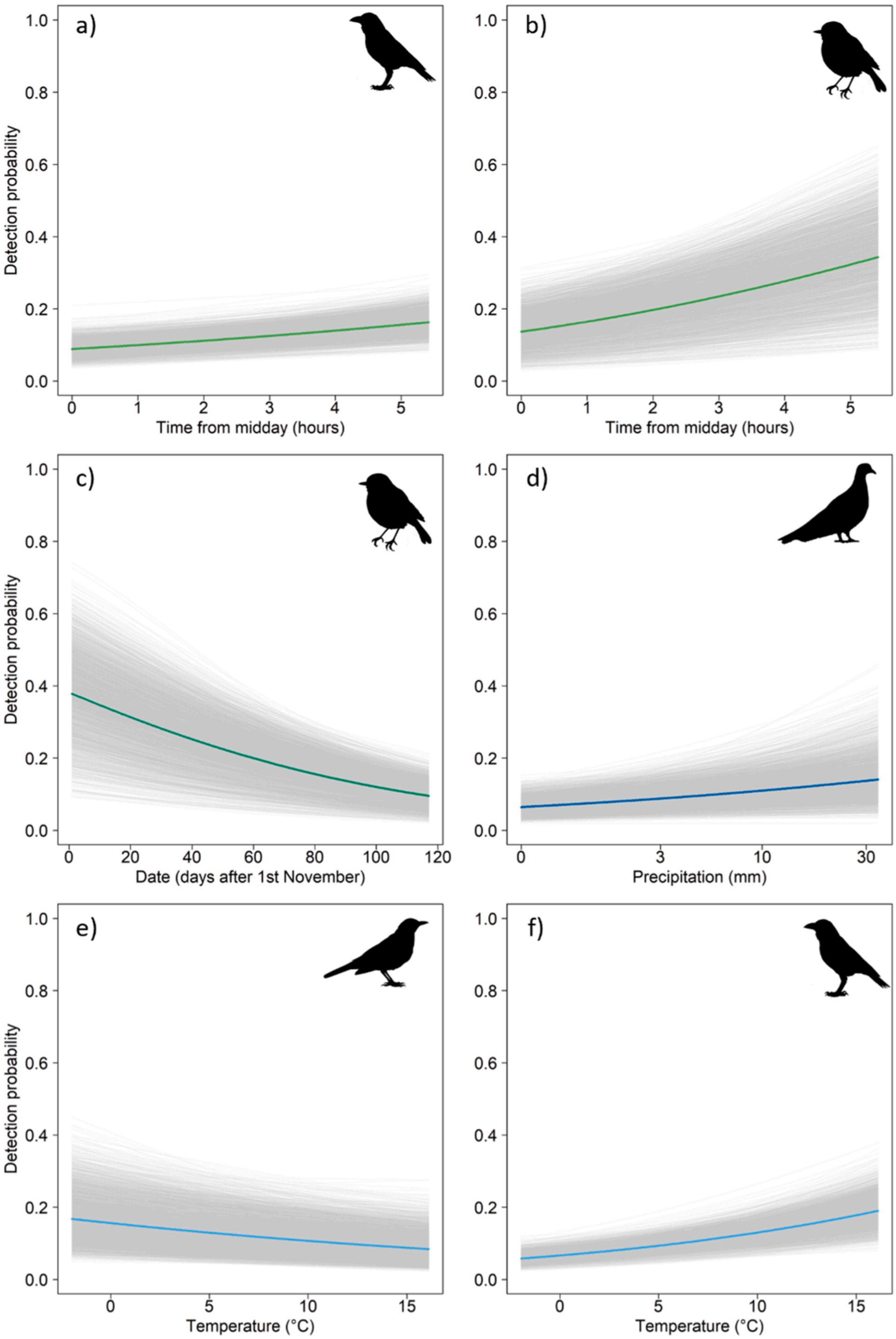

Fig. 4. Predicted relationships between detection probability and phenological (green) and weather (blue) covariates. Marginal response curves represent the relationships between: time of the day and the detection probability of a) hooded crows and b) robins; c) date and detection probability of robins; d) cumulative precipitation (24 h before the survey) and detection probability of wood pigeons; temperature (recorded during the survey) and detection probability of e) blackbirds and f) hooded crows. Thick coloured lines represent the average predicted relationships. Grey lines represent 3000 samples from the posterior distribution (1000 for each chain).

et al., 2020a). The explanatory power of detection parameters was assessed using GLMMs in a frequentist framework (Tab. S1).

All the analyses were run in R version 4.1.1 (R Core Team, 2021) using the “nimble” R package (de Valpine et al., 2017; NIMBLE Development Team, 2023). Survey data, covariates (human disturbance, weather, and phenology) and the script to analyse the data are available at figshare: https://doi.org/10.6084/m9.figshare.24518662.

3. Results

We counted a total of 1385 individuals along 68 transects (blackbird: N = 401; hooded crow: N = 555; wood pigeon: N = 143; robin: N = 286) (Table 1).

The number of people within the surveyed area varied between 3 and 952 (mean ± SD: 59.0 ± 121.9). Detection probability decreased at an increasing number of people in the park, consistently among all the species but the blackbird, whose posterior distribution widely overlapped zero (Fig. 2, Fig. 3, Tab. S2). Both hooded crows and robins were more easily detected at dawn and dusk as showcased by a positive relationship between detection probability and time of the day (expressed as absolute difference in minutes from midday; Fig. 3b-c, Fig. 4a-b). Furthermore, robins were more easily detected earlier in the season (i.e., in mid-Autumn), as shown by a negative relationship between date and detection probability (Fig. 3c; Fig. 4c). Wood pigeons had a higher probability of being detected after more rainy days (cumulative precipitation of the 24 h before the survey; Fig. 3d, Fig. 4d). Finally, temperature showed contrasting effects on the blackbird and the hooded crow, with the relationship between detection probability and temperature being negative for the former and positive for the latter (Fig. 3a-b, Fig. 4e-f). All other effects were close to zero, with 95% credible intervals widely overlapping zero, indicating no support for a relationship between the detection probability and these predictors (Fig. 3).

4. Discussion

Through repeated counts of birds in several urban parks in Northern Italy, we showed that the number of people present had a negative effect on the detection probability of most study species (hooded crow, robin, and wood pigeon). This suggests that human disturbance can be an important factor shaping the activity of birds in urban landscapes, even for species classically considered urban dwellers (Keller et al., 2020; Lardelli et al., 2022). Moreover, contextual variables such as weather and phenology often showed relevant effects on detection probability. More specifically, wood pigeons were more easily detected after rainy days, while temperature showed contrasting effects on two species: blackbirds were more easily detected at lower temperatures, while it was the opposite for the hooded crows. Hooded crows and robins had a higher detectability at dawn and dusk, thus showing a crepuscular pattern. Lastly, robins were more easily detected in the early winter than at the beginning of spring.

Individuals may finely adjust their behaviour according to the level of human disturbance, as well as other contextual variables. In this study, we showed that behavioural adaptations to human disturbance may be finely regulated by adjusting activity patterns, suggesting a key role in individual phenotypic plasticity (Gordo et al., 2021; Diamant et al., 2023). For instance, more plastic species are expected to better thrive in the urban ecosystem, suggesting phenotypic plasticity as one of the key adaptations to colonise urban areas (Capilla-Lasheras et al., 2022; Caspi et al., 2022). Human activities follow certain temporal and spatial patterns (anthropogenic clocks) and this can trigger plastic behavioural responses in urban dwelling species. In fact, the human activities schedule poses a challenge for urban birds that need to match their activities, determined by natural and endogenous clocks, with anthropogenic clocks (e.g. weekends vs. workdays; Bautista et al., 2004; Cartwright et al., 2014). The existence of such a fine match between animals’ and humans’ activity patterns has been brought up by the reduction of human activity due to the COVID-19 lockdown, when the marked disruption of anthropogenic activities caused a shift in animal activity patterns (Gordo et al., 2021; Manenti et al., 2020b). Similarly, in snow geese (*Anser caerulescens)*, during the COVID-19 lockdown, individuals reached a high body condition earlier than ever recorded (LeTourneux et al., 2021). However, body condition returned to pre-lockdown levels at the end of the lockdown (LeTourneux et al., 2023), showcasing the marked effect of a reduction in human disturbance (and hunting pressure) on urban animals.

It is then clear how human activity may disturb birds in a variety of ways, akin to the consequences of natural predation risk. For instance, recreational activities in natural areas can dramatically shape the perceived landscape of fear, with strong consequences both on the distribution (Rösner et al., 2014) and the behaviour (e.g., movement behaviour; Mumme et al., 2023). Such disturbance may be also reinforced when dogs are present: in Mediterranean areas, Kentish plovers (*Charadrius alexandrines*) flushed more when dogs (especially unleashed) were present as compared to pedestrians alone (Gómez-Serrano, 2021). Our results highlight how human disturbance may trigger a disruption in activity patterns also in urban-adapted bird species, usually predicted to be less sensitive to anthropogenic pressure (e.g., Mikula, 2014). Unexpectedly, we found no effect of the number of people on the blackbird’s detection probability. Similar results have been reported in Catalonia, where the blackbird was the only species that did not change its detectability pattern in response to the COVID-19 lockdown (Gordo et al., 2021). The blackbird, due to its high tolerance to human disturbance, is often found in urban areas (Ramellini, 2022), and has been often used as a model species to study the effect of urbanisation on birds (Fernández-Juricic and Tellería, 2000; Nordt and Klenke, 2013). Our results suggest that the blackbird might not be suitable to study the effects of human disturbance, because it may be already adapted to the urban environment. Opting for more disturbance-sensitive species could yield a more realistic and accurate portrayal of the effects of urbanisation on animal behaviour.

Phenology can strongly impact behavioural patterns of wild animals and, as a consequence, their detection probability. Such variables can greatly vary in terms of temporal scale, i.e., from daily patterns to seasonal patterns, which can both be impacted by anthropogenic activities. On the one hand, birds are usually more active at dawn and dusk (see dawn and dusk choruses; Pijanowski et al., 2011). In cities, and more generally in disturbed environments, such activity patterns may be disrupted (Shochat et al., 2006). For instance, human disturbance in cities causes a rapid shift in animals’ daily activity in order to avoid overlap with human activities

(Gordo et al., 2021). We observed this dawn and dusk peak in detectability in only two species, the hooded crow and the robin. On the other hand, seasonal dynamics (e.g. migratory movements) can affect activity patterns. We observed a decrease in the detection probability of robins throughout the season, and this may be due to the fact that individuals may be migrating towards northern Europe at the beginning of the spring (Scandolara, 2022).

In our study, we considered very common species, and this allowed us to exclude any bias due to the observer experience or rarity of the species. Observer experience has been found to affect detection of several bird species, this being particularly true for elusive species of both birds (Eglington et al., 2010; Johnston et al., 2018; Zuberogoitia et al., 2020) and other taxa such as amphibians (Schmidt et al., 2023). The species we included are normally very easily detected and highly abundant in urban parks. Hence, we can conclude that our results were likely not affected by observer experience or species' rarity. Obtaining unbiased estimates of detection probability can also aid planning and surveying activities in urban areas, aiming at optimizing economic resource allocation and maintaining the balance between human and wildlife welfare. In fact, species- and context-specific estimates of detection probability can be used to better plan surveys matching the conditions of highest detection probability. Finally, survey methods need also to be adjusted according to geographical areas, as the peak in detection probability can be influenced by geographical drivers such as latitude, longitude and time zones (Gordo et al., 2021). Hence, we advocate for more spatially representative studies including a broader number of cities and urban parks. Such studies may provide more comprehensive insights into the impacts of human disturbance on urban fauna. Nevertheless, our results can be interpreted based on the species-specific ecological characteristics and the broad variety of the life-history traits of the study species. The different guilds they belong to significantly aid the generalizability of our results, which can thus be easily extended to other urban birds, and more generally urban fauna.

In our study we focused on the non-breeding season only, and our results may change during the breeding season, when individuals, especially those of altricial species, may not be able to rapidly shift their behaviour due to the constraints imposed by breeding duties (e.g., nestling provisioning or incubation). Thus, while it is advisable to perform similar studies on different species and seasons, as they may show different responses, it is as well important to address the differences between altricial and precocial species. In this respect, full-cycle approaches may be pivotal in uncovering patterns and processes affecting detection probability and how environmental conditions affect it. Moreover, we further advocate for more extended studies addressing the variation of detection probability both in the breeding and non-breeding seasons. Such results may help in better planning of city development and management.

In conclusion, we found that human disturbance levels may trigger a fast behavioural response in urban dwelling species, suggesting a key role of phenotypic plasticity in the adaptation to urban environments. By finely tuning their activity patterns and segregating from human activities, animals may be able to coexist in human-dominated landscapes. Nevertheless, we showed that this response is species-specific, thus highlighting the importance of comparative approaches and the need for comprehensive studies to better plan city development and management.

CRediT authorship contribution statement

Mattia Falaschi: Conceptualization, Formal analysis, Writing – review & editing. **Diana Sciandra:** Investigation, Writing – review & editing. **Luca Bonomelli:** Investigation, Writing – review & editing. **Stefano Lapadula:** Conceptualization, Data curation, Investigation, Writing – original draft. **Samuele Ramellini:** Conceptualization, Data curation, Investigation, Writing – original draft.

Declaration of Competing Interest

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

Data availability

Data are uploaded on figshare at: https://doi.org/10.6084/m9.figshare.24518662

Acknowledgements

The authors would like to thank Daniele Panaretti for providing the bird silhouettes. We thank two anonymous reviewers for their comments on a previous version of the manuscript. Article processing charges were covered by the Gold Open Access Fund of the University of Milan.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e02873.

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