Rapid behavioural response of urban birds to covid-19 lockdown

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Abstract

Biodiversity is threatened by the current exponential growth of urban areas. However, it is still poorly understood how animals can cope with and adapt to these rapid and dramatic transformations of natural environments. The COVID-19 pandemic provides us with a unique opportunity to unveil the adaptive mechanisms involved in this process. Lockdown measures imposed in most countries are causing an unprecedented reduction of human activities giving us an experimental setting to assess the effects of our lifestyle on biodiversity. We studied the birds' response to the Spanish population lockdown by using more than 126,000 bird records collected by a citizen science project. We compared the occurrence and detectability of birds during the spring 2020 lockdown with baseline data from previous years in the same urban areas and dates. We found that birds did not increase their probability of occurrence in urban areas during the lockdown, refuting the hypothesis that nature has recovered its space in human emptied urban areas. However, we found an increase in bird detectability, especially during early morning, suggesting a rapid change in the birds' daily routines in response to quitter and less crowded cities. In conclusion, urban birds show high behavioural plasticity to rapidly adapt to novel environmental conditions, as those imposed by the COVID-19.

Keywords: Coronavirus disease, behavioural plasticity, urban ecology, detectability, citizen science

Running Title: COVID-19 and birds

1. Introduction

Since the first human settlements some millennia ago, the anthropogenic transformation of the natural environment to build towns and cities has been a hallmark of humanity. During the last century, urbanization has experienced exponential growth across the world and it is expected to continue as more people will move from rural to urban areas [1-4]. As a result, urbanization has become one of the most important drivers of global change and a major threat to biodiversity [2,4,6,7]. Novel, human created environments, such as urban areas, represent a formidable challenge for organisms because the magnitude and peace of the environmental alterations imposed by humans usually exceed their limits of tolerance leading to populations shrinkage and extinction [6,8]. Urban challenges include combating chemical [3], acoustic [9,10] and light pollution [11, 12], human disturbance [6,13], new pathogens [14,15] and predators [16,17], and human infrastructures [16,18]. However, some species are able to overcome these challenges and thrive in urban environments [4,8,13]. Therefore, a key question in urban ecology is how species cope with urbanization. Countless studies have demonstrated that adapting to urban environments imply some kind of phenotypical differentiation from non-urban relatives [8-10,13]. Indeed, organisms are forced to adjust their physiology, behaviour and life histories to the novel conditions imposed by the city [6,8]. However, the mechanisms underlying the differences between urban and non-urban dwellers remain largely unknown [7,8]. Observed adjustments are mostly consistent with phenotypically plastic responses [13], but individual sorting and microevolutionary changes by divergent selection could be playing a role [4,6,8]. Perhaps, our inability to disentangle these mechanisms comes from a deficit of experimental studies in urban ecology [10], in spite of the fact that human transformed environments provide often ready-made experiments. The current spread of the novel coronavirus disease (COVID-19) and its consequences represents an excellent example, as we are involuntarily involved in a major unintended social experiment.

After the declaration of the COVID-19 pandemic in March 2020 by the World Health Organization, most countries have implemented social and health measures unprecedented in recent history. These measures, aimed at containing the virus spread [19-23], have focused on social distancing and population confinement, as well as the cease of non-essential productive and social activities. Overall, the measures have contributed to a global diminishing of human activities [24]. This abrupt and dramatic disruption of most human social and economic activities have already had quantifiable effects on urban environments by marked reductions in air pollution [25-27] and noise [28,29]. One of the most noticeable and generalized measure has been applying certain degree of population lockdown, which renders our city streets empty and virtually silent. This situation provides a once-in-a-lifetime opportunity to study urban wildlife responses to less active, noisy and polluted cities and gain unprecedented mechanistic insights into how human activities affect wildlife [24,30,31]. Product of the human lockdown, unusual observations of animals in urban areas worldwide have flooded the media and the internet planting in the social imaginary the idea that "nature is getting back its space" (*sensu* [32]). Although plausible, this idea is, in most cases, based on anecdotal records, sometimes false [32], without any quantitative scientific investigation supporting such claim [24].

In this work, we aimed to assess the behavioural responses of birds to the unexpected and drastic changes occurring in urban environments resulting from the COVID-19 lockdown in a densely populated area of north eastern Spain (Catalonia). Following China [23] and Italy [20], Spain was the third country worldwide to impose a heavy population lockdown to stop COVID-19 spread. The declaration of the national emergency in March 14th 2020 by the Spanish Government imposed the strictest lockdown measures in Europe. Since then, social restrictions were alleviated progressively until the end of June (electronic supplementary material, figure S1, table S1). As in other parts of the world, this big halt of human activities has had significant environmental effects with reduced air contamination and noise in Spanish cities [26,27]. The severity of the lockdown measures imposed in Spain, make this country especially suitable to study COVID-19 lockdown effects in urban fauna, as they enjoyed exceptionally quitter and peaceful towns and cities during many weeks.

We compared bird records collected during the first four weeks of the lockdown in towns and cities of Catalonia with the available records for the same region and dates since 2015. These historical records were used as baseline data. Our broad scale approach (hundreds of study sites covering and area of 32,000 km^2) at community level (we studied 16 different species) allowed us a robust testing of two key questions:

1) Did urban birds become more common in response to human empty cities? It can be predicted that decreased human presence and disturbance allowed animals to occupy spaces that used to be above their fear tolerance thresholds [6,32]. Therefore, we expected a higher occurrence in 2020 compared to the historical records for the same urban areas. This effect being likely stronger for shier species (i.e., urban adapters), who are less tolerant to human disturbances [6,13].

2) Were urban birds more detectable as a consequence of quitter cities? It can be predicted that decreased anthropogenic noise increased the effective distance of among bird communications [6,9,10,13] and be more easily perceived by observers [33,34]. Moreover, as the masking effect of human acoustic contamination mostly disappeared, we expected an increase in singing activity, including potential shifts in its timing, to profit from the new urban soundscape [9,10,35,36]. Therefore, we expected a higher detectability of urban birds during the lockdown than in previous years, with possible changes in the daily patterns of detection.

2. Material and methods

a) Bird data

On March14th 2020, the Spanish Government declared the national emergency due to COVID-19 outbreak and imposed severe social restrictions. These restrictions included mandatory and permanent confinement of the population, borders closure, limitations in public transport, on-line education, working from home whenever possible, and closure of non-essential business and public services, such as supermarkets, pharmacies or hospitals. One day later, we launched the project "#JoEmQuedoACasa" (I stay at home) within the citizen science on-line platform *ornitho* (www.ornitho.cat). This platform aims to collect wildlife records in Catalonia (NE Spain) from birdwatchers and naturalists to improve the biodiversity knowledge of the region. *Ornitho* has been running since 2009 and has gathered more than 6.5 million records to date. The project launched during the lockdown aimed to collect information about wildlife responses to the new environmental conditions resulting from people confinement. In addition to this valuable information, the project was important to keep engaged birdwatchers in this citizen science program by encouraging them to continue complete checklists (checklist with all identified species) submission, even during a period of constrained outdoor activities [37].

Lockdown surveys were conducted between March 15th and April 13th of 2020. During these four weeks, people was subjected to the most restrictive conditions of mobility and consequently this period showed the most drastic reduction of human activities (electronic supplementary material, figure S1, table S1). Therefore, lockdown checklists were carried out only from homes (e.g., balconies, rooftops or yards) in urban environments. To determine the effect of lockdown on bird behaviour, we also gathered all complete checklists uploaded to *ornitho* recorded during the same dates between 2015 and 2019. We classified these surveyed sites as urban or non-urban according to the 2017 land use/land cover map of Catalonia [38]. Therefore, we obtained three groups of checklists: urban lockdown, historical urban, and historical non-urban, which contained a total of 126,315 bird records. Historical urban data represented baseline data, while historical non-urban data was included as control data without human disturbances.

All checklists had associated basic information about the survey: site (geographical coordinates), date, hour, time invested (which was used as a proxy for sampling effort) and observer identity. We excluded checklists lasting >3 h, as they might be discontinuous surveys. We also excluded those checklists started one hour earlier or later than dawn or sunset, respectively, as they represented nocturnal surveys. To correct for the adjustment of daylight saving time at the end of March, we rescaled recorded hours in civil time to the relevant daily sun events: dawn, noon and sunset, which were established as -1, 0 and 1, respectively. Dawn, noon and sunset were calculated for every geographical coordinate and date by the 'suncalc' library (version 0.5.0) for R software [39]. Rescaling was calculated as the quotient between the difference of noon and checklist hour and the difference of dawn or sunset and checklist hour, depending on whether checklist started earlier or later than noon, respectively. This transformation allowed to fix the small bias caused by the longitudinal differences in dawn and sunset across Catalonia as well as by the progressive day length increase during the study period. Not many observers recorded the number of individuals for each species. For this reason, we opted to work with presence/absence data.

During the lockdown, observers recorded 1,289 complete bird checklists at 149 sites. The number of replicated surveys per site and observer ranged from 1 to 91 (mean=8.7, SD=12.4). Historical records in urban areas were the scarcest: 1,062 checklists in 410 sites with up to 48 replicates per site (mean=2.6, SD=5.2). As expected, data from non-urban areas were the most abundant, as observers usually preferred birdwatching in wild habitats. We gathered 5,849 checklists from 3,113 sites. Although one observer made 84 replicates for the same site, on average, observers in this group showed the lowest site fidelity (mean replicates=1.9, SD=3.6).

We selected data for the 16 most common sedentary urban species in Catalonia [40,41] (see figure 1). We focused only on sedentary birds to avoid seasonal changes in occurrence and abundance associated with migration. Data from the common and the spotless starlings (*Sturnus vulgaris* and *S. unicolor*, respectively) were merged as *Sturnus* spp. as both were not usually identified at species level in most observations due to their high resemblance [42]. Both species are common, well spread, sympatric and share similar habits and behaviour [41]. Thus, we did not expect important differences in their occurrence or detectability.

b) Statistical analyses

To disentangle the effects of individuals' presence (first question) and detection (second question) in our bird data, we used hierarchical occupancy models [43,44]. We considered as replicated surveys those checklists reported by the same observer within the same 1x1 km UTM cell. By combining observer and location, we avoided variability in detection rates due to observer expertise. We could assume confidently that observer experience was randomly distributed across our study area. The equations defining our model were:

$$logit(\Psi_j) = \beta_0 + \beta_1 group_{Lj} + \beta_2 group_{Uj} + \beta_3 group_{Nj}$$

$$\begin{aligned} logit(\rho_i) = {} & \alpha_0 + \alpha_1 group_{Li} + \alpha_2 group_{Ui} + \alpha_3 group_{Ni} + \alpha_4 time_i + \alpha_5 time_i \cdot group_{Li} \\ & + \alpha_6 time_i \cdot group_{Ui} + \alpha_7 time_i \cdot group_{Ni} + \alpha_8 f(hour_i) + \alpha_9 f(hour_i) \\ & \cdot group_{Li} + \alpha_{10} f(hour_i) \cdot group_{Ui} + \alpha_{11} f(hour_i) \cdot group_{Ni} \end{aligned}$$

where Ψ_j is the occurrence of a species at site j and ρ_i is its detectability in the checklist i; groups *L*, *U* and *N* refer to lockdown, urban historical and non-urban, respectively; time refers to the duration of the survey; and hour refers to the starting hour. Hour was included as an unpenalized thin plate regression spline basis function (f) with five degrees of freedom because we expected that detectability could vary in a non-lineal way along the day [45,46]. Interactions between group and time and between group and hour allowed to model the effect of these two variables on detectability within each group. To test the significance of hour and interactions, we used log likelihood ratio tests. Basis functions were built by the smooth.construct function from package 'mgcv' (version 1.8-22 [47]), while occupancy models were run with the occu function of package 'unmarked' (version 0.12-3 [48]) for R.

3. Results

Probability of occurrence of a species during the lockdown did not differ significantly from the occurrence recorded in urban areas in previous years in 12 out of the 16 studied species after accounting for their imperfect detection (figure 1; electronic supplementary material, table S2). In the four species with significant differences, three increased their occurrence and one decreased it. As expected, most of the species (10) showed significant differences in their occurrence between lockdown and non-urban checklists (electronic supplementary material, table S2). On average, these species were approximately a 15% more common in the lockdown checklists than in the non-urban checklists, confirming that most of the studied species were preferentially urban dwellers.

For most species (10), probability of detection was higher in lockdown checklists than in historical urban ones, but this difference was not statistically significant in most cases (electronic supplementary material, figure S2, table S3). However, most species were less detectable in non-urban checklists than in urban ones.

As we predicted, detectability varied along the day in a non-linear way for all species (figure 2; electronic supplementary material, figure S3). Excepting two species, the pattern of daily variation in detectability was significantly different among groups (electronic supplementary material, table S4). A difference consistently found in most species was higher detectability in the first hours of the morning during the lockdown compared to the urban records from previous years (figure 2, 3). In most species, during the lockdown detectability peaked at dawn and decreased until midday, while in the historical urban checklists the peak of detectability was around mid-morning. In fact, the pattern of detectability along the day in the lockdown group resembled more to the non-urban pattern than to the urban pattern in many species. Predicted detectability at dawn by our models in the lockdown group was on average a 27% higher than in the urban group (sign test: Z=3.25, p-value=0.001; figure 3).

As expected, in all but one species, chances of detection increased with longer surveys (electronic supplementary material, figure S4, table S5). In most of them (11), such time effect was significantly different among groups (electronic supplementary material, table S4), demonstrating that increasing the sampling time does not always imply the same increase in a species' chances of detection. For half of the species, time effect was significantly lower in the lockdown group than in the historical urban group (mean reduction of 17%; electronic supplementary material, table S5). This systematic reduction contrasts with the comparison of time effect between lockdown and non-urban groups, where for nine species there were significant differences between both groups, but such differences were disparate (mean change -0.8%; electronic supplementary material, table S5).

Discussion

Birds did not occur in higher rates in towns and cities during the lockdown than before it, non-supporting the hypothesis that birds moved into the human emptied urban areas [32]. As the changes induced by the COVID-19 lockdown were drastic and sudden and did not last enough, they probably did not allow for colonization processes. The few species with a significant increase of their prevalence in urban surveys during lockdown were, interestingly, the ones that are mostly urban. As these species are not present in large numbers away from urban areas, they could hardly rely on non-urban source populations to occupy cities and towns during the lockdown.

Birds changed their detectability pattern as a consequence of the lockdown. In general, there was an increase in detection probability, which was especially marked in the early morning. As observed in non-urban habitats, detectability during the lockdown decreased from dawn onwards, while at the same urban locations detectability was historically low at dawn and increased until reaching a peak two or three hours later. It is interesting to note that the Eurasian blackbird, a model species in urban ecology studies [8,9,13,49,50], was the only exception to this pattern. Overall, many species showed a "wilder" pattern of detection during the lockdown in urban areas.

Urban birds during lockdown may have shown this detectability peak at dawn, typical of non-urban habitats, because of a rapid behavioural response to adapt to the new environmental conditions imposed by the COVID-19 measures [51]. Birds rely heavily on acoustic communication. During reproduction, males sign to attract females and defend their territories, becoming highly conspicuous and detectable. COVID-19 lockdown was imposed just at the beginning of the breeding season, when singing activity was expected to be especially high [52]. Therefore, there was a strong pressure to time singing activity to the optimal moment of the day. This moment is dawn because the physical properties of the atmosphere enhance acoustic transmission [53,54] and consequently, birds can reach the maximum audience. Thus, urban birds during the lockdown may have advanced their main period of singing activity to dawn, increasing their detection at those hours, similar to what is observed in non-urban areas.

During the lockdown, human presence and activities decreased drastically (electronic supplementary material, figure S1, table S1), being this especially notable during rush hour, which virtually disappeared [27]. During the spring in Spain, morning rush hour matches with the first hours of light, when birds are expected to be especially communicative [36,50,55]. The dramatic decrease in noise during the lockdown released early morning acoustic space that could be recovered by the dawn chorus. Empirical and experimental evidence demonstrates that urban birds avoid the masking effect of anthropogenic noise [9,10,35,36,56]. Our findings match these previous studies, but instead of advancing the dawn chorus [36,49,50,57], our historical urban data suggests that birds would delay their peak of activity (and consequently of detectability) to mid-morning. In our study context, this can be explained because civil and solar time are heavily decoupled in Spain since the country is located in the westernmost part of its time zone [58]. For this reason, if birds in Catalonia advance their activities before sunrise, they would be still suffering an important overlap with morning noisy human activities, such as commuting, school attendance, shop opening, etc. [50,55]. Hence, the best option for birds would be to delay the peak of activity to after the morning rush hour [56]. Moreover, most of the previous studies have been carried out in more northern latitudes [9,49,59], where climate conditions can still be severe at night in early spring. Under these circumstances, individual survival can be challenged by a strong nocturnal energy demand [60,61]. There, dawn singing can become a relevant and honest signal of phenotypic quality of males, as only those individuals in best physical condition can undergo dawn fasting [49]. In Mediterranean regions, where spring nights are mild, the role of dawn singing as signal of male quality might be less important. Attracting mates would be the prime objective for singing and consequently, males would be more pressed to place this activity when interference of anthropogenic noise is at its lowest. Since sunrise, these lowest levels of noise are just after the morning rush hours (i.e. later than 9 a.m.), when the air physical properties still keep sound attenuation and fluctuation low [53].

If birds have changed their behaviour, this adaptive, flexible behavioural response must have been mediated by phenotypic plasticity. Lockdown was sudden and the environmental scenario in urban areas changed radically from one day to the next (electronic supplementary material, figure S1) [27]. This unprecedented social experiment imposed by the COVID-19 allowed us to test and support the hypothesis of the high plasticity displayed by individuals living in urban areas in order to cope with a constantly changing environment [6-8,51]. However, this fast adaptive response might have been facilitated by a previous conditioning of birds to weekly rhythms of human activities. Birds change their behaviour from working to weekend days [35,56,62] to match with human behaviours. Therefore, birds could assimilate the lockdown as a very long and especially peaceful weekend. Nevertheless, it would be interesting to explore the long-lasting consequence at a community level of this environmental change [59]. Weekends are just two days long, while strict people lockdown lasted for at least two months in most regions of Spain. One may speculate that bolder and fast-adapting species would adapt their behaviour on a weekly basis. However, during the lockdown, all species had enough time to adapt to the long-lasting new conditions. In fact, as we have demonstrated, all of them modified their daily patterns of detectability. Maybe the most urbanite species have benefited the least of this lockdown as their boldness and higher human tolerance was no longer an advantage in empty cities.

In addition to the birds' rapid behavioural response to the anomalous environmental conditions during the lockdown, observers had certainly enhanced opportunities to detect birds during this period. Urban areas were quitter than usual [27-29], improving the chances of listening the birds [32-34,53]. Moreover, absence of people outdoors allowed for the display of shy and distrustful behaviours [6], facilitating bird observations, especially for those less singing species, as the magpie *Pica pica* or the yellow-legged gull *Larus michahellis*. However, these improved conditions for urban birdwatching were heavily constrained by the fact that observers were forced to stay at their homes and their sampling area was reduced to what they could see from their balconies, yards or rooftops. Therefore, improved detection was to some extent counterbalanced by the limited scope from the survey sites. The observed effect in increased sampling time would support this hypothesis, as we demonstrated that the discovery rate in most species was slower during the lockdown surveys than in the historical urban ones.

The differences observed between urban and non-urban environments were expected as habitat configuration and bird densities are patently different between them. In fact, populations of urban exploiter birds show usually higher densities in cities than in rural or natural close areas [6-8], facilitating their detection in urban areas. Such differences may have serious consequences for monitoring schemes aiming to quantify wildlife occurrence and abundance by standardized protocols, as the assumption of equal detectability under similar circumstances is usually violated [33,44,45,63]. For instance, one sampling hour at dawn is not equivalent in terms of chances to detect a species in urban and non-urban habitats. Traditional protocols assume that the best moment to detect birds is early morning [53,64], which is actually true, but apparently only in natural conditions without human disturbance, as we have demonstrated here (see figure 2). If the detectability peak in most urban populations is reached at mid-morning, their abundance would be systematically underestimated by usual sampling protocols based on early morning bird surveys. As there is an increased awareness about the importance of urban bird populations [40], it is necessary to ensure its accurate quantification, which may imply a redefinition of the most popular current census techniques [8]. Additionally, in this work we demonstrated the utility of occupancy models and the necessity to account for imperfect detection [45,46].

The COVID-19 lockdown is revealing the stress, noise and pollution present in urban areas [25,26,28,29]. Under normal conditions, bird behaviour is altered and the possibility to enjoy the natural values of our cities is notably diminished [8]. Our society should reflect on our urban lifestyle and how it affects welfare of urban fauna and jeopardizes its conservation. As the world is becoming more urbanized and animals will be forced to live more often in anthropogenic environments [6-8], one way to ensure their adaptation as urban dwellers would be by reducing our nosier and more disturbing activities. Most importantly, not only urban populations of non-human animals would be benefited, but also ourselves from quitter, more peaceful and less polluted cities.

Authors' contributions

G.G. has the original idea and designed the monitoring program. O.G. and G.G. formulated formal hypotheses, and collected and arranged the necessary data for the study. O.G. analysed data. O.G. wrote the manuscript, with contributions from all the authors.

Competing Interest

The authors declare no competing interests.

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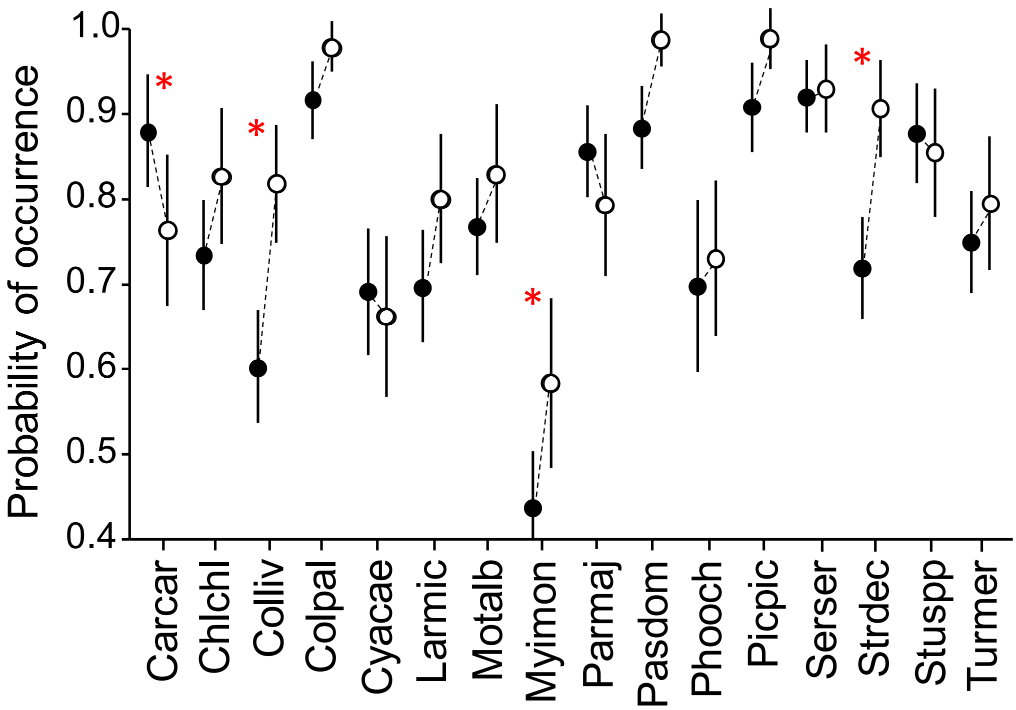

Figure 1. Probability of occurrence of birds in urban areas before (2015-19, black dots) and during (2020; white dots) the COVID-19 lockdown. Asterisks indicate significant differences (*p*-value < 0.05). Error bars denote 95% confidence intervals. Acronyms for the species: Carcar *Carduelis carduelis*, Chlchl *Chloris chloris*, Colliv *Columba livia*, Colpal *Columba palumbus*, Cyacae *Cyanistes caeruleus*, Larmic *Larus michahellis*, Motalb *Motacilla alba*, Myimon *Myiopsitta monachus*, Parmaj *Parus major*, Pasdom *Passer domesticus*, Phooch *Phoenicurus ochruros*, Picpic *Pica pica*, Serser *Serinus serinus*, Strdec *Streptopelia decaocto*, Stuspp *Sturnus* spp., Turmer *Turdus merula*.

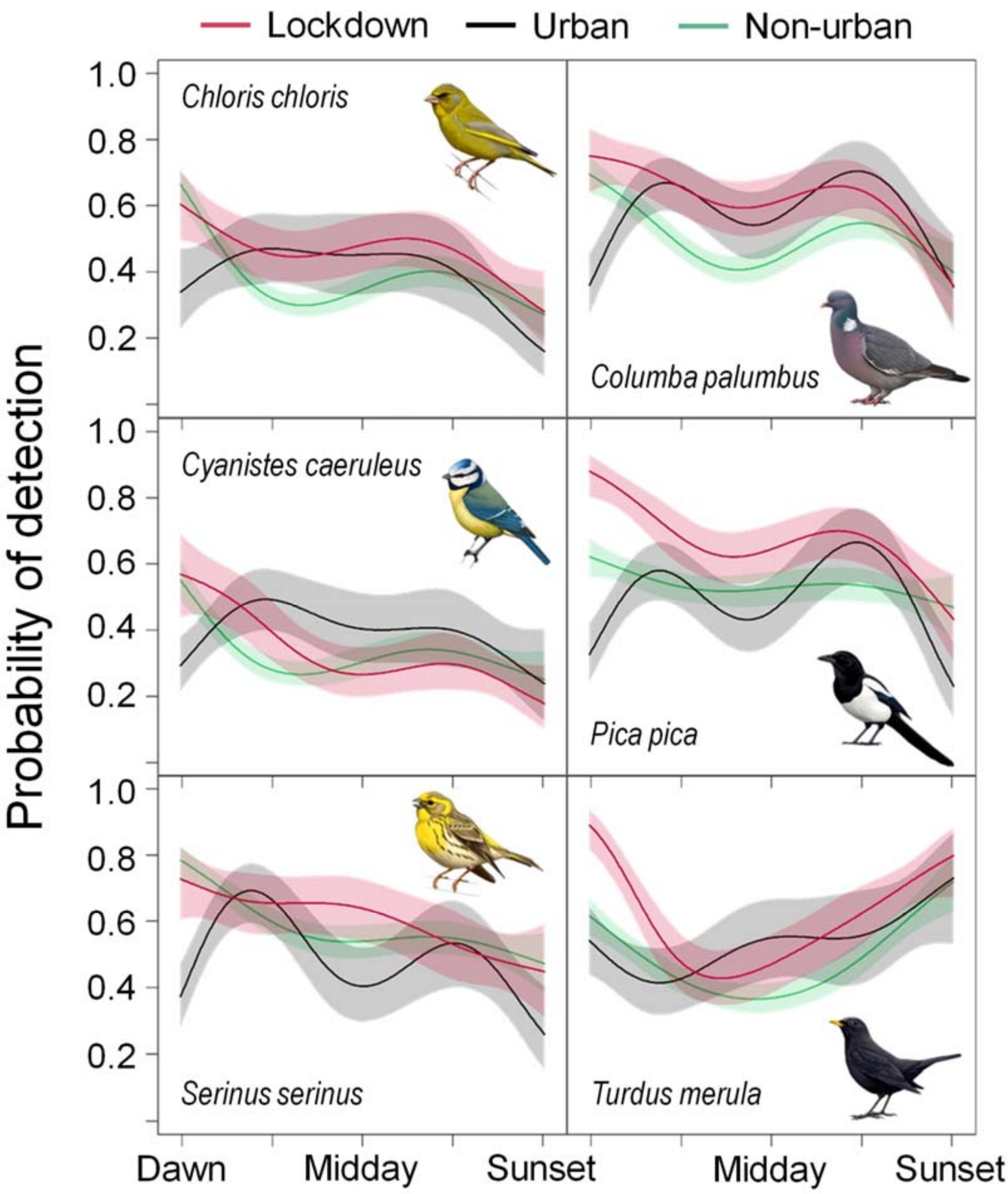

Figure 2. Variation in the probability of detection along the day for each group of data (collected during the lockdown, collected historically in urban sites, and collected in non-urban environments). Shaded areas represent the 95% confidence intervals. See fig. S2 in the electronic supplementary material for the rest of species. Bird illustrations by Martí Franch/Catalan Ornithological Institute.

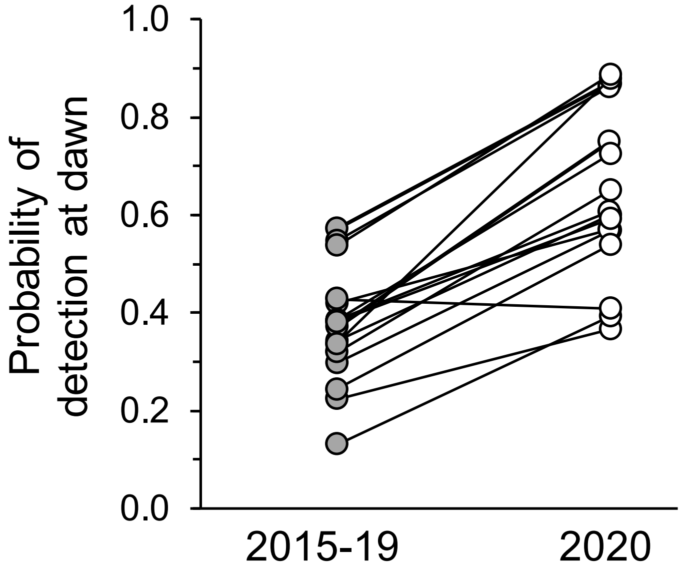

Figure 3. Probability of detection in urban environments at dawn for the 16 studied bird species before (2015-19) and during (2020) COVID-19 lockdown.

Electronic supplementary information for this manuscript include the following:

Figure S1. Variation in people's visiting habits to six categories of places in Catalonia between March 1st and July1st.

Figure S2. Probability of detection of birds in urban areas before and during the COVID-19 lockdown

Figure S3. Variation in the probability of detection along the day for each group of data in 10 studied species.

Figure S4. Effect of sampling time on the probability of detection for each group of data.

Table S1. Percentage variation in people's visiting habits to six categories of places between March 15th and April 14th in Catalonia and its provinces.

Table S2. Results of the occupancy part of the occupancy models.

Table S3. Results for group effects on the detection part of the occupancy models.

Table S4. *P*-values for the effects of hour, the interaction between hour and group, and the interaction between time and group in the occupancy models

Table S5. Results for the effects of the interaction between time and group on the detection part of the occupancy models.

ELECTRONIC SUPPLEMENTARY INFORMATION for:

RAPID BEHAVIOURAL RESPONSE OF URBAN BIRDS TO COVID-19 LOCKDOWN

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Figures S1 to S5

Tables S1 to S4

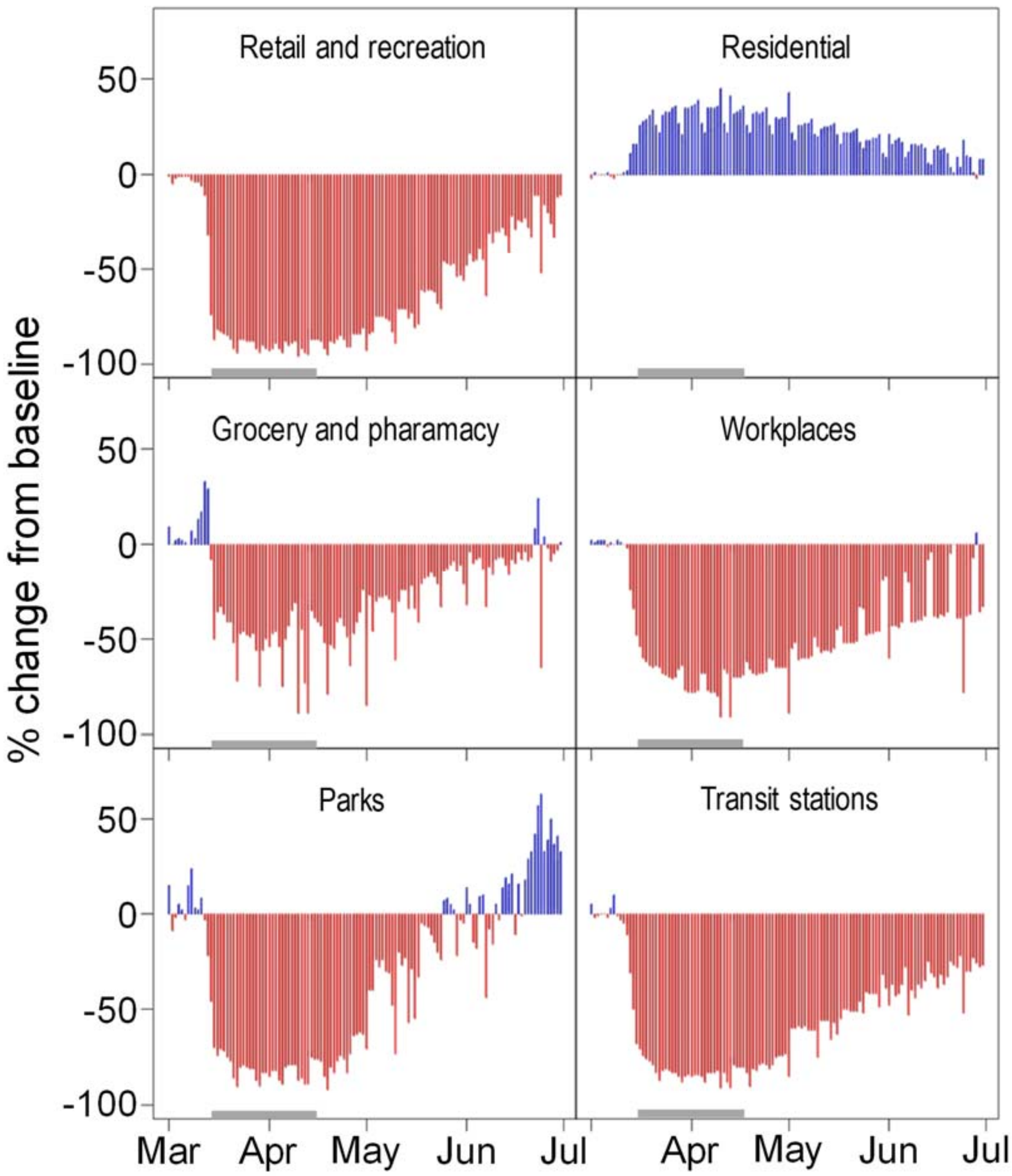

Figure S1. Variation in people's visiting habits to six categories of places in Catalonia between March 1st and July1st. These graphs can be interpreted as a proxy for human activity. To improve visualization, negative deviations are shown in red and positive in blue. The grey band on to the x axis shows the period of bird data collection. The emergency state in Spain due to COVID-19 lasted from March 15th to June 21st. Note the forced strict lockdown during the first two months of this period and the following progressive recovery of activities. Figure data are freely available from "*Google COVID-19 Community Mobility Reports*" (https://www.google.com/covid19/mobility/ Accessed: August 25th 2020). Baseline level (i.e., 0%) has been calculated as the average from January 3rd to February 6th 2020 (visit the previous link for further technical details on data calculations).

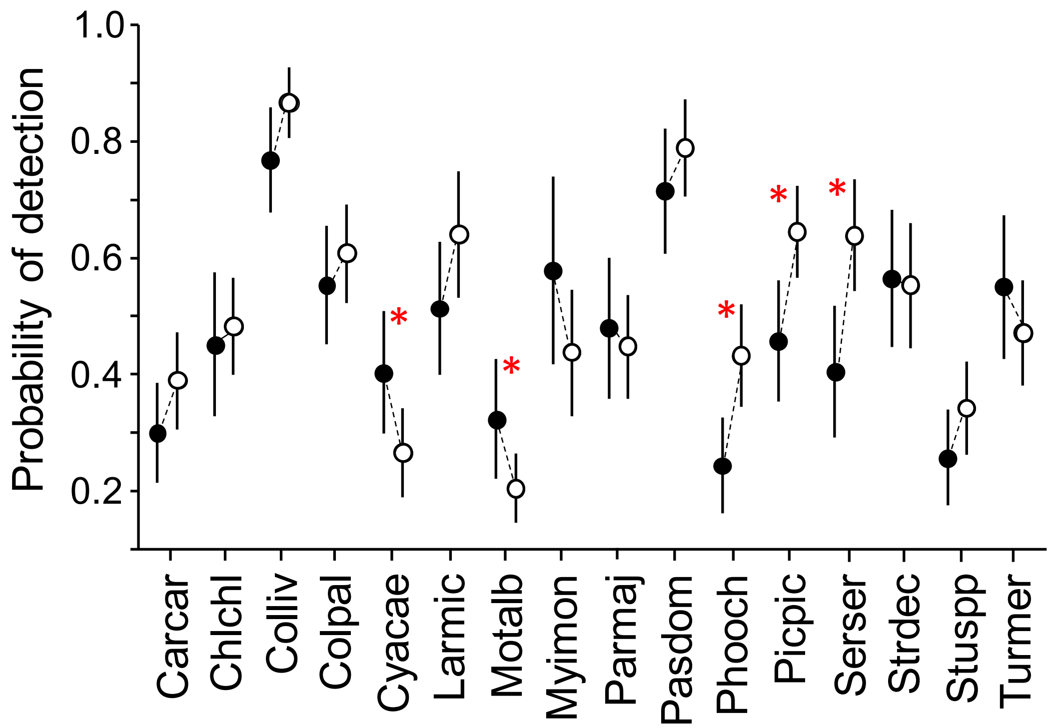

Figure S2. Probability of detection of birds in urban areas before (2015-19, black dots) and during (2020; white dots) the COVID-19 lockdown. Asterisks indicate significant differences (*p*-value < 0.05). Error bars denote 95% confidence intervals. Acronyms for the species: Carcar *Carduelis carduelis*, Chlchl *Chloris chloris*, Colliv *Columba livia*, Colpal *Columba palumbus*, Cyacae *Cyanistes caeruleus*, Larmic *Larus michahellis*, Motalb *Motacilla alba*, Myimon *Myiopsitta monachus*, Parmaj *Parus major*, Pasdom *Passer domesticus*, Phooch *Phoenicurus ochruros*, Picpic *Pica pica*, Serser *Serinus serinus*, Strdec *Streptopelia decaocto*, Stuspp *Sturnus* spp., Turmer *Turdus merula*.

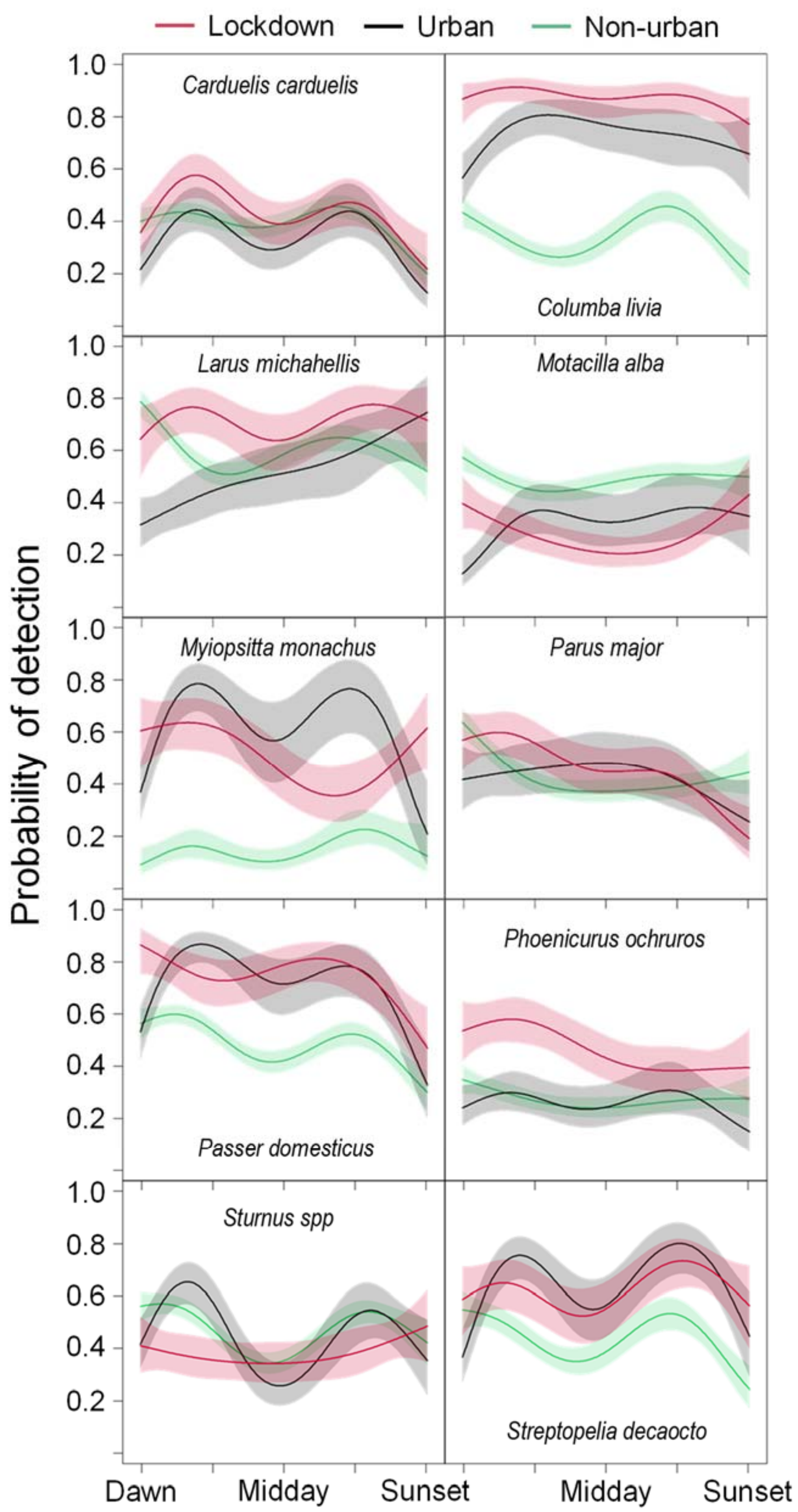

Figure S3. Variation in the probability of detection along de day for each group of data (collected during the lockdown, collected historically in urban sites, and collected in non-urban environments). Shaded areas represent the 95% confidence intervals.

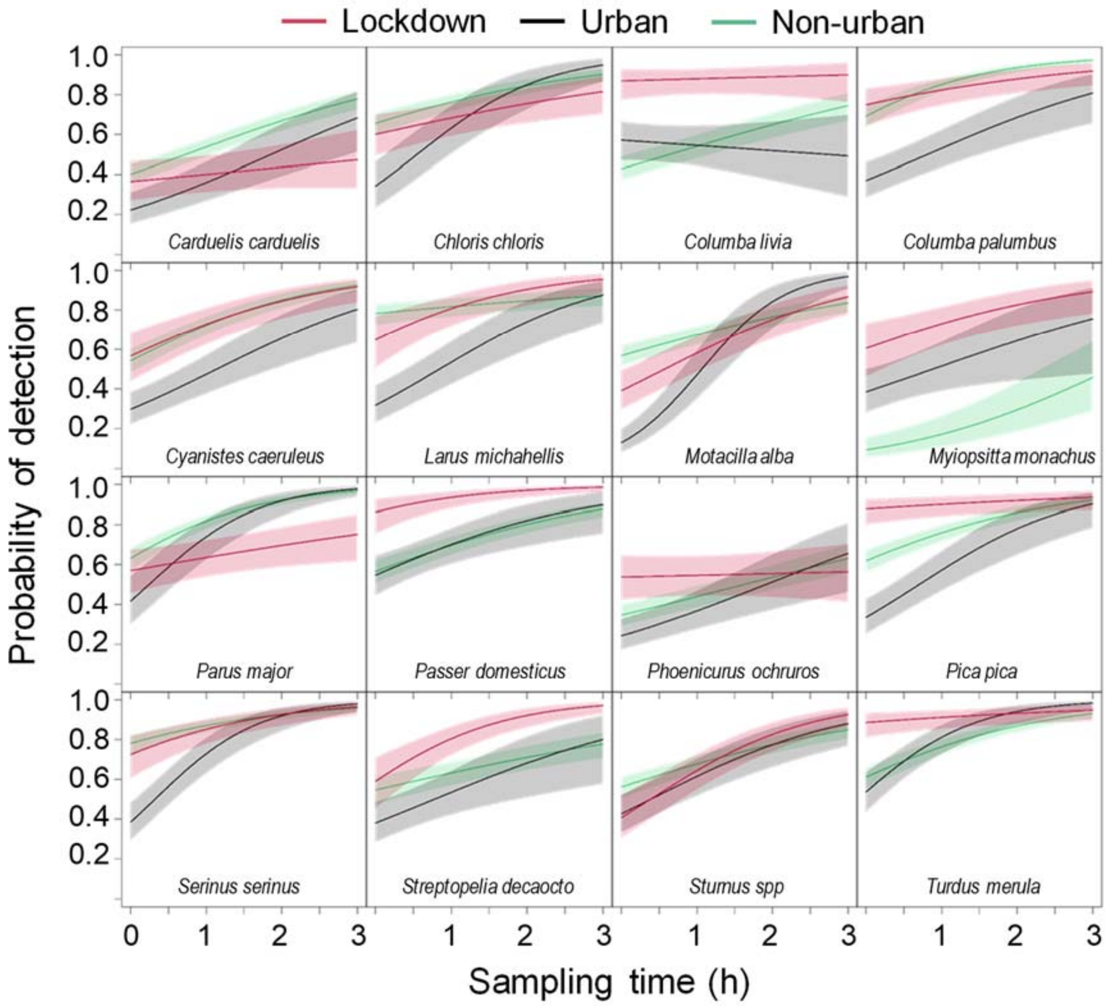

Figure S4. Effect of sampling time on the probability of detection for each group of data (collected during the lockdown, collected historically in urban sites, and collected in non-urban environments). Predictions done for surveys started at dawn. Shaded areas represent the 95% confidence intervals.

Table S1. Percentage variation in people's visiting habits to six categories of places between March 15th and April 14th in Catalonia and its provinces. The values show the average of daily deviations from the baseline level. Outdoor sites experienced a severe decline, while people stayed more at home. See figure S1 for details.

Place	Catalonia	Barcelona	Girona	Lleida	Tarragona
Retail and recreation	-89.56	-90.41	-88.13	-86.19	-88.56
Grocery and pharmacy	-51.28	-53.13	-51.59	-52.72	-53.06
Parks	-81.34	-83.59	-74.22	-62.63	-76.63
Transit Stations	-82.41	-82.44	-80.41	-78.88	-83.00
Workplaces	-70.41	-72.22	-64.22	-61.81	-65.69
Residential	31.25	32.03	28.41	26.00	27.84

Table S2. Results of the occupancy part of the occupancy models. *Naïve* columns show the proportion of sites where the species was found during the surveys, i.e. the raw occurrence without correction for the imperfect detection of birds. *Estimate* columns show the estimated occurrence of the studied species once the detectability was accounted for. As expected, estimated occupancy was always higher than the observed (i.e., *naïve*), demonstrating both imperfect and variable detection of birds. For the urban and non-urban groups of historical data (2015-19), a column with the differences (Δ) between their estimates and the lockdown group (2020 data) estimates is provided. The *p*-values for these differences are also shown. Values <0.05 are in bold. At the bottom of the table, the average and standard deviation of the studied species are given.

Species	**Lockdown (2020)**		**Urban (2015-19)**		**Δ lockdown-urban estimates**	***p***	**Non-urban (2015-19)**		**Δ lockdown-non-urban estimates**	***p***
	naïve	estimate	naïve	estimate			naïve	estimate		
European goldfinch, *Carduelis carduelis*	0.5973	0.7635	0.5634	0.8795	-0.1160	**0.0457**	0.5401	0.8435	-0.0800	**0.0677**
Greenfinch, *Carduelis chloris*	0.6779	0.8263	0.5537	0.7342	0.0921	0.1020	0.4055	0.6759	0.1504	**0.0056**
Rock pigeon, *Columba livia*	0.7718	0.8176	0.4683	0.6024	0.2152	**0.0001**	0.2501	0.4582	0.3593	**<0.0001**
Wood pigeon, *Columba palumbus*	0.8859	0.9781	0.7463	0.9158	0.0623	0.0695	0.6645	0.8511	0.1270	**0.0044**
Blue tit, *Cyanistes caeruleus*	0.5235	0.6616	0.4693	0.6906	-0.0290	0.6364	0.3792	0.6144	0.0472	0.3670
Yellow-legged gull, *Larus michahellis*	0.7481	0.8001	0.5428	0.6970	0.1031	0.0565	0.4929	0.6851	0.1150	**0.0159**
White wagtail, *Motacilla alba*	0.6376	0.8292	0.6049	0.7675	0.0618	0.2520	0.4899	0.7377	0.0915	0.0735
Monk parakeet, *Myiopsitta monachus*	0.5041	0.5833	0.3580	0.4373	0.1460	**0.0187**	0.1300	0.3243	0.2590	**<0.0001**
Great tit, *Parus major*	0.6443	0.7924	0.6642	0.8548	-0.0624	0.2060	0.6126	0.8221	-0.0296	0.4840
House sparrow, *Passer domesticus*	0.9195	0.9863	0.7677	0.8837	0.1025	0.0633	0.5480	0.7649	0.2213	**0.0092**
Black redstart, *Phoenicurus ochruros*	0.5705	0.7306	0.3585	0.6975	0.0330	0.6350	0.2965	0.6426	0.0879	0.1090
Magpie, *Pica pica*	0.8658	0.9879	0.7311	0.9076	0.0803	0.1770	0.5328	0.7040	0.2839	**0.0215**
Serin, *Serinus serinus*	0.8389	0.9295	0.7732	0.9198	0.0097	0.7790	0.6200	0.7851	0.1444	**0.0017**
Collared dove, *Streptopelia decaocto*	0.8322	0.9052	0.5980	0.7189	0.1863	**0.0005**	0.2842	0.4578	0.4474	**<0.0001**
Starling, *Sturnus spp*	0.6980	0.8538	0.6479	0.8774	-0.0235	0.6250	0.5010	0.7480	0.1058	**0.0342**
Eurasian blackbird, *Turdus merula*	0.6846	0.7941	0.6073	0.7494	0.0447	0.3890	0.5754	0.7853	0.0088	0.8380
mean	*0.7125*	*0.8275*	*0.5909*	*0.7708*	*0.0566*		*0.4577*	*0.6813*	*0.1462*	
SD	*0.1308*	*0.1139*	*0.1316*	*0.1332*	*0.0882*		*0.1521*	*0.1516*	*0.1399*	

Table S3. Results for group effects on the detection part of the occupancy models. For the urban and non-urban groups, a column with the differences (Δ) between their estimates and the lockdown group estimates is provided. The *p*-values for these differences are also shown. Values <0.05 are in bold. At the bottom of the table, the average and standard deviation of the studied species are given.

Species	**Lockdown (2020**	**Urban (2015-19)**	**Δ lockdown-urban**	***p***	**Non-urban (2015-19)**	**Δ lockdown-non-urban**	***p***
European goldfinch, *Carduelis carduelis*	0.3897	0.3002	0.0895	0.1444	0.3948	-0.0051	0.9133
Greenfinch, *Carduelis chloris*	0.4820	0.4517	0.0303	0.6938	0.3469	0.1351	**0.0049**
Rock pigeon, *Columba livia*	0.8665	0.7688	0.0978	0.0716	0.3289	0.5376	**<0.0001**
Wood pigeon, *Columba palumbus*	0.6070	0.5535	0.0534	0.4289	0.4302	0.1768	**0.0005**
Blue tit, *Cyanistes caeruleus*	0.2658	0.4035	-0.1377	**0.0364**	0.3036	-0.0378	0.4140
Yellow-legged gull, *Larus michahellis*	0.6405	0.5131	0.1274	0.1182	0.5865	0.0540	0.3912
White wagtail, *Motacilla alba*	0.2052	0.3233	-0.1181	**0.0419**	0.4716	-0.2664	**<0.0001**
Monk parakeet, *Myiopsitta monachus*	0.4378	0.5773	-0.1395	0.1640	0.1097	0.3281	**<0.0001**
Great tit, *Parus major*	0.4479	0.4803	-0.0324	0.6730	0.3717	0.0762	0.1290
House sparrow, *Passer domesticus*	0.7891	0.7150	0.0740	0.2820	0.4224	0.3667	**<0.0001**
Black redstart, *Phoenicurus ochruros*	0.4321	0.2437	0.1885	**0.0028**	0.2414	0.1907	**<0.0001**
Magpie, *Pica pica*	0.6452	0.4573	0.1879	**0.0058**	0.5259	0.1192	**0.0169**
Serin, *Serinus serinus*	0.6385	0.4040	0.2345	**0.0027**	0.5393	0.0993	0.0810
Collared dove, *Streptopelia decaocto*	0.5525	0.5649	-0.0124	0.8790	0.3876	0.1648	**0.0092**
Starling, *Sturnus spp*	0.3426	0.2574	0.0852	0.1510	0.3534	-0.0108	0.8140
Eurasian blackbird, *Turdus merula*	0.4717	0.5500	-0.0783	0.3100	0.3683	0.1034	**0.0394**
mean	*0.5134*	*0.4728*	*0.0406*		*0.3864*	*0.1270*	
SD	*0.1789*	*0.1508*	*0.1182*		*0.1167*	*0.1830*	

Table S4. *P*-values for the effects of hour, the interaction between hour and group, and the interaction between time and group in the occupancy models. *f* refers to the basis function used to model the non-lineal effect of hour on bird detectability.

Species	*f*(hour)	*f*(hour)*group	time*group
European goldfinch, *Carduelis carduelis*	<0.00001	0.14308	0.04767
Greenfinch, *Carduelis chloris*	<0.00001	0.00291	0.02069
Rock pigeon, *Columba livia*	0.00754	0.00137	0.04995
Wood pigeon, *Columba palumbus*	<0.00001	0.00001	0.93144
Blue tit, *Cyanistes caeruleus*	<0.00001	0.00002	0.94749
Yellow-legged gull, *Larus michahellis*	0.00256	0.00001	0.00328
White wagtail, *Motacilla alba*	0.09982	0.00018	0.00001
Monk parakeet, *Myiopsitta monachus*	0.00455	0.00008	0.83579
Great tit, *Parus major*	<0.00001	0.00113	0.00023
House sparrow, *Passer domesticus*	<0.00001	0.00073	0.64000
Black redstart, *Phoenicurus ochruros*	0.01681	0.11286	0.05613
Magpie, *Pica pica*	0.00048	0.00009	0.02690
Serin, *Serinus serinus*	<0.00001	0.00027	0.01794
Collared dove, *Streptopelia decaocto*	0.00003	0.00039	0.02776
Starling, *Sturnus spp*	<0.00001	0.00594	0.04043
Eurasian blackbird, *Turdus merula*	<0.00001	0.00464	0.00649

Table S5. Results for the effects of the interaction between time and group on the detection part of the occupancy models. Columns lockdown, urban and non-urban show the probability of detection of the species after 1 hour of survey. A probability of 0.5 means that the observers may or may not detect the species with the same probability (i.e. flat slope). Except the rock pigeon in urban checklists, in all cases, as expected, these probabilities were above 0.5 (i.e., increased probability of detection of a species throughout sampling time). For the lockdown estimates, the *p*-value testing whether or not this slope was different from 0.5 is shown. However, in urban and non-urban groups, the *p*-value shows whether or not these slopes differed from the lockdown group. The difference (Δ) between these slopes is also provided to enhance result interpretation.

Species	**Lockdown (2020)**	***p***	**Urban (2015-19)**	**Δ lockdown-urban**	***p***	**Non-urban (2015-19)**	**Δ lockdown-non-urban**	***p***
European goldfinch, *Carduelis carduelis*	0.5372	0.1908	0.6620	-0.1248	**0.0019**	0.6345	-0.0973	**0.0012**
Greenfinch, *Carduelis chloris*	0.5889	**0.0023**	0.7675	-0.1786	**0.0002**	0.6282	-0.0394	0.2063
Rock pigeon, *Columba livia*	0.5250	0.6086	0.4735	0.0515	0.4093	0.6112	-0.0862	0.0861
Wood pigeon, *Columba palumbus*	0.6805	**<0.0001**	0.6757	0.0048	0.9130	0.6920	-0.0115	0.7310
Blue tit, *Cyanistes caeruleus*	0.6710	**<0.0001**	0.6800	-0.0091	0.8400	0.6863	-0.0154	0.6480
Yellow-legged gull, *Larus michahellis*	0.6936	**0.0001**	0.7120	-0.0184	0.7438	0.5537	0.1399	**0.0061**
White wagtail, *Motacilla alba*	0.6839	**<0.0001**	0.8566	-0.1726	**0.0001**	0.6107	0.0733	**0.0130**
Monk parakeet, *Myiopsitta monachus*	0.6371	**0.0008**	0.6298	0.0073	0.9110	0.6685	-0.0314	0.4990
Great tit, *Parus major*	0.5682	**0.0197**	0.7988	-0.2306	**<0.0001**	0.7243	-0.1560	**<0.0001**
House sparrow, *Passer domesticus*	0.6983	**0.0001**	0.6602	0.0381	0.5410	0.6384	0.0599	0.2120
Black redstart, *Phoenicurus ochruros*	0.5089	0.7519	0.6446	-0.1357	**0.0019**	0.5965	-0.0876	**0.0041**
Magpie, *Pica pica*	0.5584	0.0532	0.7258	-0.1674	**0.0005**	0.6599	-0.1014	**0.0021**
Serin, *Serinus serinus*	0.6862	**<0.0001**	0.8111	-0.1248	**0.0114**	0.6536	0.0327	0.4020
Collared dove, *Streptopelia decaocto*	0.7411	**<0.0001**	0.6514	0.0897	0.1240	0.5881	0.1530	**0.0006**
Starling, *Sturnus spp*	0.7244	**<0.0001**	0.6823	0.0421	0.3050	0.6212	0.1032	**0.0013**
Eurasian blackbird, *Turdus merula*	0.5705	**0.0234**	0.7883	-0.2178	**<0.0001**	0.6726	-0.1021	**0.0018**