Breeding in the pandemic: short-term lockdown restrictions do not alter reproductive decisions and avian life-history traits in a European capital city

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Abstract

Humans are transforming natural habitats into managed urban green areas and impervious surfaces with unprecedented pace. Yet the effects of human presence *per se* on animal life-history traits are rarely tested. This is particularly true in cities, where human presence is often indissociable from urbanisation itself. The onset of the SARS-CoV-2 outbreak, along with the resulting lockdown restrictions, offered a unique, “natural experiment” context to investigate wildlife responses to a sudden reduction of human activities. We analysed four years of avian breeding data collected in a European capital city to test whether lockdown measures altered nestbox occupancy and life-history traits in two urban adapters: great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*). Lockdown measures, which modulated human presence, did not influence any of the life-history traits inferred. In contrast, tree cover, a distinct ecological attribute of the urban space, positively influenced clutch size, a key avian life-history and reproductive trait. This highlights the importance of habitat and food webs over human activity on animal reproduction in cities. We discuss our results in the light of other urban wildlife studies carried out during the pandemic, inviting the scientific community to carefully interpret all lockdown - associated shifts in biological traits.

Keywords: lockdown, SARS-CoV-2, urbanisation, human presence, avian life-history traits, tree cover

1. Introduction

Humans, the ecosystem engineers *par excellence*, are capable of quickly transforming original habitats into managed green areas and impervious surfaces – such as buildings, infrastructural networks and other built-up structures[1]. Hence, human-driven ecological impacts are pervasive globally, and are amplified in size relative to human biomass: for this reason, humans are also identified as the "hyper-keystone species"[2].

Ever since the Industrial Revolution, and especially over the past few decades, human ecosystems were characterised by an exponential growth of cities and towns worldwide, along with a parallel migration of people from semi-natural, rural and marginal areas, to more urbanised settlements[3,4]. Along with the urbanisation process, the footprint of human activities is now influencing all dimensions of the natural world, and is an undeniable threat to biodiversity [3,5–7]. As such, cities are a valuable case study of ecological and evolutionary change as they rapidly induce novel and selective pressures on animal and plant communities [8]. These may respond by disappearing (urban avoiders), spreading (urban exploiters) or thriving / surviving (urban adapters) within these novel environments [9–11]. Urban adapters, such as great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*), became valuable study systems to determine, on one hand, whether urban populations differ from their rural counterparts in terms of genotype, physiology or behaviour and - on the other - to define the main components of the urban landscape causing such variation [12]. Earlier studies reported pronounced differences in terms of life-history traits and reproductive success between urban and rural populations [12], often identifying chemical [13,14], light [15,16] and sound pollution [17,18] as main drivers of these differences. Other studies emphasized the negative and pervasive effect of built up areas, infrastructural networks and, more generally, impervious surfaces on avian fitness [19–21]. Yet, only a handful of studies tested whether human presence *per se* was linked to evolutionary traits in urbanised contexts [21,22].

A considerable limitation in studying the effects of human presence *per se* on wildlife across the urban mosaic stems from the unfeasibility to disassociate human presence from urbanisation in general, which is a wider and more complex ecological process. Consequently, it was impossible to date to exclude the constant presence of humans from urban areas – where "crowds" are the norm, and where fine-scale heterogeneity of human presence in the urban mosaic is also known to be repeatable over time and space [23] (but see [24–26]). Nevertheless, the presence of humans in urban green areas overlaps with the breeding season of many avian species able to thrive within these novel environments. Given such overlap in terms of space use between humans and wildlife across the urban mosaic, how would free living - populations respond in terms of life-history strategy to a sudden disappearance of the "human component" from normally highly frequented areas? Even though such question could be perceived as utopian until recently, 2020 proved us wrong.

Along with the spread of the novel coronavirus disease, the World Health Organization (WHO) declared the SARS-CoV-2 – zoonotic pandemic on the 11th of March 2020 [27]. This kick-started a cascade of governmental actions worldwide aimed at containing the virus transmission [28]. Most of these were realised through the cancellation of public events and the immediate interruption of any type of gatherings characterised by high human densities, be it commercial or social events. Although the timing and strength of lockdown restrictions imposed by each government differed between countries, quarantine and stay-at-home orders considerably reduced the use of public transports and the flow of people within and outside of cities during the first pandemic wave of infections, creating newly emptied soundscapes even where crowds and chaos were the *routine* [29]. This new realm, defined as the "*Anthropause*", offered a unique opportunity for scientists to investigate wildlife-responses to lockdown-measures in urban landscapes, while – for the first time ever - retaining humans indoors, leaving the outdoors emptied from their hyper key-stone species [30] (**Table 1**).

Shortly after the SARS-CoV-2 outbreak, media outlets started to report unusual sightings of animal species never observed in cities; similarly, social media were flooded with photos of wildlife in the urban space. An equally remarkable effort was made by the scientific community, which investigated, (to the best of lockdown regulations for any specific region), the possible impact of the pandemic on wildlife biology by collecting data in the field or through the observations of volunteers (i.e. citizen-science projects and online platforms, **Table 1**). To date, the majority of studies here reported (9 out of 13, **Table 1**) conducted on the effect of the SARS-CoV-2 lockdown focused on behavioural patterns of animal communities, specifically in terms of sightings [31–33]. Analyses were generally performed by comparing pre-lockdown and post-lockdown periods for the recorded observations, and emphasized an increased trend for uncommon "species occurrence" in areas where humans suddenly disappeared (e.g. [31,32,34]). However, these reports were not uniform across all species: in some cases, no difference pre- and during lockdown was noted [31,32,34], while in other cases, the directionality of the association was opposite (e.g., fewer sightings were reported during than before lockdown) [31,34]. For instance, some urban exploiters during lockdown decreased in number within certain urban areas: such changes may be related to the "absence" of human-generated food resources caused by this novel circumstance [34]. Moreover, along with the discoveries on SARS-CoV-2 origin, other studies reported a negative attitude of people towards bats [35]. This aspect turned into a direct persecution of this animal taxon across China, which was subsequently defined as "Ecological culling" [35]. These results suggests that more data is needed to delineate trait - and species-specific responses to SARS-CoV-2 lockdown restrictions across human-modified landscapes.

As the majority of studies reporting the impact of human lockdown on wildlife during the SARS-CoV-2 pandemic relate to behavioural traits, data on the impact on animal life-history and / or reproductive traits remains very scarce [32,33,36]: in fact, despite the presumed beneficial effects of lockdown on urban wildlife, only two studies (out of the 13 here described) to date report a positive association between reproductive traits and implemented lockdown measures (e.g., increased hatching success in Leatherback sea turtles *Dermochelys coriacea* [33], and increased clutch size in common swifts *Apus apus* [32]). The implications of the "*Anthropause*" on wildlife life-history variation in urban populations remain therefore largely unexplored. To address this knowledge gap, we tested whether lockdown restrictions introduced during the SARS-CoV-2 pandemic in a European capital city (Warsaw, Poland) were associated with changes in occupancy patterns and life-history trait variation in two nestbox-breeding passerines: great tits *Parus major* and blue tits *Cyanistes caeruleus*. Thanks to a legal framework allowing scientists to work when needed during the pandemic, and to ascertain the possible role of lockdown measures on free-living populations, the same data collection protocole was used in 3 years prior to the SARS-CoV-2 pandemic (2017-2019) and during the pandemic (2020).

The life-history traits investigated here included nestboxes occupancy, laying date, clutch size and incubation duration: we focused on these traits because all of them occurred within the period of the strictest lockdown measures in Poland, which lasted from the 1st until the 20th of April, 2020 [37–39]. In parallel to testing the effect of lockdown measures on avian trait variation, we also analysed the role of tree cover in nestbox surroundings – a considerably less labile attribute of the urban space than human presence, and vital in providing shelter and food resources (*i.e.* caterpillars as favourite prey item [40]) in these two species.

Based on previous work on human presence carried out in natural and urbanised contexts [21,22], but in contrast to media reports on the impact of lockdown on urban wildlife, we did not expect any association between lockdown measures and avian reproductive life-history traits. Conversely, we predicted that the percentage of tree cover in nestbox surroundings would maintain its influence on great tit and blue tit life-history trait variation regardless of the pandemic.

2. Methods

2.1 Study sites and lockdown restrictions in Poland

Avian life-history and reproductive data were collected from 2017 to 2020 across seven study sites set in a gradient of urbanisation in the capital city of Warsaw, Poland. Each study site is characterised by an assigned number of Schwegler woodcrete nestboxes (type 1b, with a 32 mm entrance hole and erected in a 50m-distance grid) suitable for great tits and blue tits. The study system here described aims to accurately reflect the urban matrix, as it comprises a wide range of diverse and contrasted habitat patches [41].

While a state of epidemic was officially declared in Poland on March 20th, a series of increasingly restrictive measures limiting human presence outdoors were subsequently introduced. A strict lockdown period forbidding the use of urban green areas was introduced between the 1st of April and 20th of April included. During this time, city dwellers were not allowed to access urban green areas, recreational locations, natural reserves or protected areas within and outside city borders. The only allowed activities outside of homes included the purchase of food supplies and other essentials items, caring duties and work, which enabled the authors of this study to access green areas within the remit of their work.

Study areas in our urban study system were thus subjected to contrasted levels of access restrictions during the SARS-CoV-2 lockdown. We consequently assigned each study site to the following categories:

- "Lockdown - Entrance Allowed" (LEA) – pertains to 4 sites and a total of 173 nestboxes; included streets and residential areas where residents were allowed outdoors to fulfil their essential needs during the pandemic
- "Lockdown – Entrance Not Allowed" (LENA) – pertains to 3 sites and a total of 236 nestboxes; included parks, woodlands and forest reserves, all of which were closed to the public during the strict lockdown period. All these sites re-opened to the public on the 20th of April 2020.

We provide a brief description with lockdown information (as "LEA" or "LENA") below; sites are listed from the most distant to the closest to Warsaw city centre. More details on each study site can be found in Corsini et al [21,42] and Szulkin et al. [41].

A. Suburban village (n=47 nestboxes, LEA). Palmiry village (20º46'48.9748''E - 52º22'11.3382''N) is located c. 20 km away from Warsaw city centre and borders Kampinos National Park (Site B). Palmiry is a typical suburban village, where residential homes with gardens are interconnected by tree-lined avenues.

B. Natural forest (n=110, LENA). Kampinos National Park (20º47’14.3867’’E - 52º21’22.5409’’N) is a large forest located c. 20 km from Warsaw city center. The area is characterised by pine and mixed oak-pine forest habitats.

C. Residential area II (n=52, LEA). Osiedle Olszyna neighbourhood (20º57’39.37097’’E - 52º16’23.71883’’N) is a block of flats intermixed with green spaces and recreational facilities. It borders with the urban woodland “Las Olszyna” (site D).

D. Urban woodland (n=21, LENA). Las Olszyna (20º57’33.93652’’E - 52º16’10.55093’’N) is a green space that includes a deciduous, wet alder forest and an open space with an adjacent playground.

E. Office area (n=28, LEA). The Warsaw University “Ochota” Campus (20º59’8.85224’’E - 52º12’43.77676’’N) is located next to the urban park Pole Mokotowskie (site G) and belongs to one of the central districts of the city. Buildings consist of university offices, laboratories and other student facilities.

F. Residential area I (n=46, LEA). The “Muranow” neighbourhood (20º59’5.74332’’E - 52º14’52.17925’’N) is a residential area, similar in design to Residential area II (site C).

G. Urban park (n=105, LENA). Pole Mokotowskie (21º0’6.98321’’E - 52º12’46.66874’’N) is an extensive urban green area located close to the city center. With its alternation of meadows, tree-covered areas and recreational structures (i.e. playgrounds and sport facilities), it provides a centrally-located recreational area for city dwellers.

2.2 Avian life-history traits data collection

From the end of March, we checked nestboxes weekly to identify those occupied by great tits and blue tits. A nestbox was considered as “occupied” when at least one egg was laid on a completed nest. Weekly checks allowed to record the date of the first egg laid (e.g. laying date recorded from the 1st of April, corresponding to the value of 1), incubation duration (given in days and calculated as: hatch date – first egg laid date – clutch size – 1, [43], though incubation occasionally starts earlier or later than clutch completion in tits [44]) and clutch size (total number of eggs in the nest). Only first broods were included in the analyses [45].

2.3 Tree-cover measurements

We measured the percentage of tree cover in a 100m radius around each nestbox following Szulkin et al. [41]. Briefly, after downloading a raster layer from Copernicus Land Monitoring Services (https://land.copernicus.eu/ sitemap;Forests/Tree Cover Density), we processed the data in qGIS (v.2.18.25). The map of tree cover was generated in 2015 and contained a 20m-pixel resolution layer. After creating a 100m radius buffer around each nestbox, we obtained the averaged value of tree cover (in %) at the nestbox level using the function *Zonal Statistics* in qGIS.

2.4 Statistical analyses

Statistical analyses were performed within the computing environment R (v.3.6.2), separately for great tits and blue tits, in order to directly assess species-specific trait variation.

2.4.1 Association between avian life-history traits and lockdown restrictions

To test associations between avian life-history traits and lockdown restrictions, all tests were run in a model averaging framework [46]. To test the effect of lockdown on avian traits investigated in this study, we specifically focused on the interaction between *year* and *lockdown status* (LEA - Lockdown Entrance Allowed *vs.* LENA - Lockdown Entrance Not Allowed sites), the latter explicitly reflecting a lack of outdoors human activity in LENA sites in 2020.

To model nestbox occupancy, we fitted generalised linear models (GLMs) with binomial distribution ("*glm*" function in the R-package "*lme4*" v.1.1-21-[47]). A nestbox was considered occupied (1) only if a great tit or a blue tit (analysed separately) was breeding in the nestbox. Nestbox occupancy (0/1) was fitted as binomial-response variable in each model, while the interaction between the two categorical variables *year* (four levels: 2017, 2018, 2019 and 2020) and *lockdown status* (two levels: LEA and LENA study sites) were fitted as predictors.

To model variation in egg laying date ("Lay date"; the egg laying date of a nest where the first egg was laid on the 1st of April would be coded with the value of 1), we fitted Linear Mixed Effects models (LMMs) with Gaussian distribution ("*lmer*" function in the R-package "*lme4*"). As for the analysis of nestboxes occupancy, the interaction between the two categorical variables *year* and *lockdown* status were fitted as explanatory variable. To control for variation associated with site specificity, the categorical variable *study site* (sites A-G) was fitted as random effect. The same model structure was used to model variation in clutch size, where we additionally fitted *lay date* as explanatory variable to control for the fact that earlier clutches in the season are often larger than later ones [48].

For incubation duration, we ran Generalised Linear Models with Gaussian distribution ("g*lm*" function in R; the random effect of *study site* was not added here due to singularity problems in the model and a lack of model convergence when the random effect was added). Incubation duration was fitted as response variable while the interaction between *year* and *lockdown status*, and the continuous-variable *lay date* (to control for seasonal differences in each breeding event, as incubation duration decreases later in the season [21]) were fitted as predictors.

2.4.2 Association between avian life-history traits and tree cover

To test whether tree cover in a 100 m radius around each nestbox (in %) covaries with avian life-history traits, the following models were run:

For nestbox occupancy, we used the same structure as described in 2.4.1, but for the variable *lockdown status*, which was replaced by the continuous variable *tree cover*.

In lay date and clutch size models, we used Generalised Linear Models (GLM) fitting each response with a Gaussian distribution. Similarly to the models ran on occupancy detailed above, the interaction between *year* and *tree cover* were fitted as predictors. Additionally, the explanatory variable *lay date* was added to clutch size and incubation duration analyses to mirror analyses performed on the same response variables as detailed in 2.4.1. In contrast to analyses described in the section 2.4.1, *site* was not included as random effect, as it covaries with the variable *tree cover* (here fitted as key explanatory variable).

2.4.3 Does lockdown influence tree cover preferences in occupied nestboxes?

To test whether tit tree cover preferences in occupying specific nestboxes changed due to the reduced human presence that occurred in 2020, we performed a one-way ANOVA test to model *tree cover* as a function of year among occupied great tit and blue tit nestboxes..

3. Results

3.1 No association between lockdown restrictions and avian life-history traits

There was no significant association between pandemic-related human space use (tested as the interaction *lockdown status*year*) and any of the life-history traits inferred (Table S1, Table 2, Figure 2). In contrast, year and lockdown status (but not their interaction) influenced blue tit and great tit life-history traits, bearing in mind that lockdown status largely reflected sites that are either places of work or residence *vs.* green spaces (LEA *vs*. LENA sites, respectively; Table 2; Table S3).

Nestbox occupancy rates, measured in percentage, were significantly lower in "Lockdown - Entrance Allowed" (LEA) sites relative to "Lockdown – Entrance Not Allowed (LENA) sites in blue tits (Figure 2, Table S4). Considerable year to year variation was detected, with occupancy rates significantly higher in 2018 and 2019 relative to 2017 in great tits (Table 2). An equally strong year-effect was confirmed for *lay date* in both species: in fact, in 2018, 2019 and 2020, lay date was delayed relative to 2017 (Table 2). Even though the averaged model kept the interaction between lockdown categories and year in both species, confidence intervals for the lockdown effect (*lockdown status* * *Year 2020*) always included zero (Table S1, Table 2). Moreover, there was a significant reduction in clutch size later in the season in both species (Table 2) and in great tits, the number of eggs per breeding attempt was also significantly lower in 2020 relative to 2017. The only significant interaction included the categorical variables "*Year 2019*" and "*Lockdown (LEA)*", which was positively associated with clutch size in great tits (Table S1, Table 2). In both species, incubation duration was shorter in 2018, 2019 and 2020 relative to 2017, and decreased later in the season (Table S1, Table 2).

3.2 Tree cover as driver of avian life-history traits

In both great tits and blue tits, tree cover around the nestbox positively covaried with clutch size, but not with other traits (Figure 3; Table 3, Table S2). For all traits, *tree cover* * *year* interactions were either dropped from the final models or overlapped zero, confirming a lack of between-year variation of the effect of tree cover on life-history traits in both species. In blue tits, clutches were initiated later in the season in areas with the highest percentage of tree cover (Table S2, Table 3): a similar trend, yet not significant, was found in great tits. Mirroring results reported in 3.1, there was also considerable variation in life-history traits induced by year, and a reduction in incubation duration later in the season for both species (Table S2, Table 3).

3.3 Averaged tree cover around occupied nestboxes did not change in the pandemic

Tree cover surrounding occupied nestboxes did not differ in the pandemic year when compared to other years (Table S5).

4. Discussion

We did not detect any significant *lockdown status*year* interaction on occupancy or on any reproductive life-history traits investigated. In line with earlier work demonstrating limited effects of human presence on avian reproduction in the urban space [21], this study finds no evidence for an effect of the 2020 pandemic lockdown on blue tit or great tit life-history reproductive variation (Table 2). Instead, year effects were the key drivers of occupancy and life-history trait variation in these two urban adapters (Table 2), suggesting the overarching role played by other biotic and abiotic factors on reproductive trait variation during the pandemic. In contrast to a lack of effects of human presence (previously demonstrated in Corsini et al. [21], and, here, “experimentally” through the testing of the *lockdown status * year* interaction in this study), we established that tree cover consistently covaried positively with clutch size in both great tits and blue tits (Figure 3; Table 3). The most likely proximate factors underlying this relationship are tree-dwelling lepidopteran larvae and other insects, which remain the main food items used by adult tits to feed their offspring in urban-dominated landscapes [40] (but see [49] reporting that blue tits may occasionally use human-generated food resources to feed their nestlings [6]). Consequently, tree cover appears to act as cue for resource allocation in reproductive decisions.

The absence of lockdown-related effects in terms of avian life-history traits in our study system mirrors the findings of a study of human presence performed at a fine spatial scale in 2017 within two areas of the same study setup [21]. The authors reported how human presence in a 15 meters radius around the nestbox was not associated with any of the avian life-history traits inferred. In contrast, other elements of the urban landscape (such as distance to roads and paths) influenced incubation duration and nestlings body mass 15 days after hatching [21]; see also [19]. Here, we used use the “*Anthropause*” [30] triggered by the SARS-CoV-2 pandemic, and set in the context of avian breeding data collected across multiple years in a heterogeneous urban landscape, to confirm the limited role of human presence with a “quasi” experimental approach, strengthening the above-mentioned findings. Interestingly, the extent of tree cover surrounding occupied nestboxes did not change in the pandemic year relative to previous years. As humans disappeared from LENA sites in 2020, these unique circumstances could have prompted birds to settle in nestboxes that would have otherwise been avoided because of too high human densities, which are also known to covary with low levels of tree cover in the urban space [41]. This suggests that birds are selecting their breeding locations irrespective of human physical presence, and that the ecological cues such as tree cover used by tits in their reproductive decisions remains unchanged irrespective of the *Anthropause* (Table 3, Figure 3).

Recent studies to date report a mixed picture of the impact of the SARS-CoV-2 pandemic lockdown on wildlife biological variation (Table 1). Out of a prevalence of behavioural studies (largely reporting a presence or absence of particular species during the lockdown period, Table1), only three studies present phenotype or fitness data, specifically in the leatherback turtle [33], the greater snow goose [36] and the common swift [32]. Thus, Manenti et al. [32] report an increase in clutch size in the common swift in Italy during the pandemic. The authors attribute this positive trend in reproductive success to the drastic drop of air pollution recorded in 2020 in the country (specifically, nitrogen dioxide, benzene and sulphur dioxide [50]). In particular, nitrogen dioxide is known to reduce insects' biomass and to directly affect birds fitness by inhalation exposure [50,51]. Differently to tits, which feed on canopy invertebrates during the breeding season [40], common swifts are aerial Afro-Palearctic migratory birds, which exclusively feed on aerial insects [52], and may thus be more likely to changes in aerial insect abundance in the urban space, though this relationship remains speculative. Another study reported possible pandemic-driven changes in the body condition of the greater snow goose (Table 1). Variation in body condition was discussed in the context of a reduction of the hunting activity in the area of study during the lockdown period [36]. Consequently, the reduced stress generated by the lower number of scaring events, contributed to the increased body condition in greater snow geese in 2020 [36], with possible downstream consequences on reproductive success (e.g., number of fledglings) later in the season [36]. Other wildlife studies carried out in the SARS-CoV-2 pandemic period (Table 1) highlight the role of food availability in species occurrence [34,53]: thus, species such as Feral pigeons (*Columba livia*) and Torresian crows (*Corvus orru*) (often referred to as "urban exploiters" as they rely on waste, bread, seeds and other anthropogenic food resources [9,53]) decreased in number within the urban space since the pandemic started, moving to more natural areas to feed on native invertebrate communities, with serious (and, to some extent, destructive) consequences on local ecosystems [53]. All in all, results reported to date highlight a species-specific response to lockdown restrictions (Table 1).

As mentioned above, another example of species-specific responses related to breeding preferences in tits, includes the nesting behaviour: in fact, great tits and blue tits are cavity-nesters and as such, are not directly exposed to humans or dogs (often associated with human presence in urban areas [23]) during the breeding season. It is possible that data from open and/or ground-nester birds could reveal a more complex picture of lockdown-effects associated with human presence on avian breeding success. On one hand, human presence may expose certain ground and open nesting birds to predation by domestic animals especially in urban green areas, where cats and dogs are often left free to roam. Consequently, their absence from urban green areas during the SARS-CoV-2 pandemic could lead to a lower number of dog-related predation events. Conversely - the presence of humans in cities may acts as a deterrent towards other urban predators such as foxes *Vulpes vulpes*, squirrels *Sciurus vulgaris*, martens *Martes foina* or birds of prey, etc). Undoubtedly, lockdown timing, combined with biological attributes of species biology (e.g. diet or breeding preferences), might have played a role in the contrasted breeding output recorded during the pandemic. More lockdown studies would be valuable to reliably explore the fine-scale dynamics between human presence and wildlife biological variation in this unusual period of cities under lockdown.

Scientists worldwide used ground-based and citizen-science data to quantify behavioural, phenotypic and fitness responses of urban wildlife to the outdoors absence of humans in cities (Table 1), which ultimately demonstrated even far-reaching downstream relationships between the two: for example, the SARS-CoV-2 pandemic led to a decrease of road kill events across multiple taxa (see [32,54], Table 1). This is most likely caused by the lower number of vehicles allowed to travel during the lockdown periods. Moreover, while, in some cases, reduced hunting activity improved animals body condition [36], in other cases the pandemic increased poaching events [55]. Thus, human activities responses to the lockdown measures were also context-related.

5. Conclusions

The short-term restrictions imposed by the SARS COV2 pandemic lockdown did not alter variation in occupancy rates or reproductive life-history variation in great tits and in blue tits in the capital city of Warsaw. Our results, together with those reported in recent studies (Table 1), point to a complex picture of lockdown consequences on urban wildlife, which are likely to be species-specific (e.g related to diet or breeding preferences), and context-related (e.g. dependent on the location and timing of lockdown or of human responses to it).

We argue that a replicated attempt to analyse long-term studies in the specific context of the "*Anthropause*" generated by the SARS-CoV-2 pandemic would reveal a fuller and more balanced picture of the diverse urban wildlife responses than what was reported in media outlets. Ultimately, such studies would pave the way to i) a better understanding of rapid life-history and behavioural responses of wildlife to human activities and ii) the implementation of new conservation strategies to preserve biodiversity, even in areas where human presence is now the norm.

Data accessibility:

In case of manuscript acceptance, data here analysed will be available in Dryad public repository.

Authors' contribution:

MC: conceptualization, data collection, data curation, formal analysis, visualization, writing original draft. ZJ, MW, MR, IS, EM: data collection, data curation, manuscript editing. MS: conceptualization, data collection, data curation, manuscript editing.

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Table 1. Overview of studies examining the impact of Covid19-lockdown restrictions on wildlife and on human wildlife-related activities.

Study species	Traits/ human actions tested[a]	Effect[b]	Study area / habitat type	Methods[c]	Lockdown period[d]	Ref.
Greater snow goose	Scaring events (HA)	(-)	Small agricultural island	G	16th of March – 4th of May 2020	36
(*Chen caerulescens atlantica*)	Body condition (PH&F)	(+)	Saint-Lawrence estuary	G		
	Hunting activities (HA)	(-)	[Canada]	G		
Avian species	Presence (B)	(nd)	Urban and rural areas [north eastern Spain]	CZS	15th of March – 13th of April 2020	56
	Morning detectability (B)	(+)	Urban and rural areas [north eastern Spain]	CZS		
Avian species	Submission of protocol lists to SABAP2 (HA)	(-)	[South Africa]	CZS	27th of March – 30th of April 2020	57
	Participation to “Lockdown-gardens” surveys (HA)	(+)		CZS		
Eurasian tree sparrow (*Passer montanus*)	Flight Initiation Distance (B)	(-)	Urban areas [China]	G	[ns]	58
Puma (*Puma concolor*)	Presence (B)	(+)	[North American urban centres]	CZS	[1st of March – 31st of July 2020]	31
Coyote (*Canis latrans*),	Presence (B)	(nd)	[North American urban centres]	CZS		
Moose (*Alces alces*)	Presence (B)	(nd)	[North American urban centres]	CZS		
American black bear (*Ursus americanus*)	Presence (B)	(nd)	[North American urban centres]	CZS		
Bobcat (*Lynx rufus*)	Presence (B)	(nd)	[North American urban centres]	CZS		
Feral pigeons (*Columba livia*)	Presence (B)	(-)	Urban - open food centres - Singapore	G	7th of April – 1st of June 2020	34
Feral pigeons (*Columba livia*)	Foraging and moving (B)	(+)	Urban – foraging hotspots - Singapore	G		
Feral pigeons (*Columba livia*)	Resting (B)	(-)	Urban – foraging hotspots - Singapore	G		
Javan myna (*Acridotheres javanicus*)	Presence (B)	(+)	Urban – refuse collection centre - Singapore	G		
Javan myna (*Acridotheres javanicus*)	Presence (B)	(-)	Urban – green areas - Singapore	G		
Common myna (*Acridotheres tristis*)	Presence (B)	(nd)	Urban - open food centres - Singapore	G		
House crow (*Corvus splendens*)	Presence (B)	(nd)	Urban – foraging hotspots - Singapore	G		
Torresian crows (*Corvus orru*)	Presence (B)	(-)	Urban	G	2nd of April – 30th of June 2020	53

	Presence (B)	(+)	Rural / natural	G		
White crowned sparrow	Amplitude of song (B)	(-)	San Francisco Bay [United States of America]	G	1st of April – 31st of May 2020	29
(Zonotrichia leucophrys)	Noise levels (HA)	(-)	San Francisco Bay [United States of America]	G		
	Song performance (B)	(+)	San Francisco Bay [United States of America]	G		
Leatherback sea turtle	Presence (B)	(+)	Beach on the North Caribbean coast [Costa Rica]	G	1st of March – 31st of August 2020	33
(*Dermochelys coriacea*)	Hatching success (PH&F)	(+)	Beach on the North Caribbean coast [Costa Rica]	G		
Crested porcupine (*Hystrix cristata*)	Presence (B)	(+) / (nd)	Urban areas / non – urban areas [Italy]	CZS	11th of March – 4th of May 2020	32
Kentish plover (*Charadrius alexandrinus*)	Presence (B)	(+)	Seaside [Italy]	G		
Water birds	Species richness (B)	(+)	Artificial lake [northern Italy]	G		
Common swift (*Apus apus*)	Clutch size (PH&F)	(+)	[Italy]	G		
Common toads (*Bufo bufo*)	Road kill (HA)	(-)	[Italy]	G		
Agile frog (*Rana dalmatina*)	Road kill (HA)	(-)	[Italy]	G		
Common wall lizard (*Podarcis muralis*)	Road kill (HA)	(-)	[Italy]	G		
Western green lizard (*Lacerta bilineata*)	Road kill (HA)	(-)	[Italy]	G		
Eastern cottontail (*Sylvilagus floridanus*)	Diurnal activity (B)	(+)	[northern Italy]	G		
Wildlife	Poaching activities (HA)	(+)	Protected areas [Nepal]	G	24th of March – 21st of June 2020	55
	Presence (B)	(+)	Protected areas [Nepal]	G		
Bats species	Negative attitude from the public (HA)	(+)	[China]	CZS	[ns]	35
Hedgehog (*Erinaceus roumanicus*)	Road kill (HA)	(-)	Chełm [Poland]	G	[ns]	54

Table 1. Overview of studies conducted in 2020 testing the influence of lockdown restrictions on wildlife. ([a]) categorises the examined traits as behavioural (B; note that here, "behaviour" is not qualified as phenotype as this category is largely constituted of species sightings rather than individual-specific attributes), individual-level phenotype and fitness (PH&F) or to wildlife-related human activities (HA). Effects ([b]) reports the directionality of the association driven by the

lockdown period, denoted as an increase (+), decrease (-) or no significant difference (nd). Methods of data collection detailed in ([c]) categorise data collection as performed by scientists during fieldwork (FW) while CZS relates to the contributions of volunteers (e.g. a citizen science approach), which recorded daily-based observations through online or other social media platforms . ([d]) indicates the length of the lockdown period, where "ns" indicates "not specified" in the study).

Species	Response	Variable	Estimate	se	CI 95%	Relative importance
Great tit	Occupancy	(Intercept)	-1.794	0.158	-2.103; -1.484	
n = 1636		*Year*				1.00
(1 = 364; 0 = 1272)		**Year 2018**	**0.510**	**0.190**	**0.137; 0.882**	
		Year 2019	**0.479**	**0.191**	**0.106; 0.853**	
Family: Binomial		Year 2020	0.336	0.194	-0.045; 0.717	
		Lockdown status (LEA)	-0.249	0.133	-0.510; 0.012	0.68
Blue tit	Occupancy	(Intercept)	-1.471	0.125	-1.716; -1.225	
n = 1636		*Year*				0.3
(1 = 251; 0 = 1385)		Year 2018	-0.070	0.188	-0.438; 0.298	
		Year 2019	-0.391	0.199	-0.782; 0	
Family: Binomial		Year 2020	-0.163	0.191	-0.537; 0.211	
		Lockdown status (LEA)	**-0.505**	**0.146**	**-0.791; -0.220**	1.0

Species	Response	Variable	Estimate	se	CI 95%	Relative importance
Great tit	Lay date	(Intercept)	10.542	1.113	8.497; 12.589	
n = 290		*Year*				-
		Year 2018	**9.108**	**1.194**	**6.737; 11.392**	
Family: Gaussian		**Year 2019**	**6.540**	**1.202**	**4.176; 8.853**	
Random: Study site		**Year 2020**	**7.574**	**1.220**	**5.191; 9.937**	
		Lockdown status (LEA)	2.707	1.684	-0.384; 5.917	-
		*Lockdown status * Year*				-
		Lockdown status * Year 2018	-2.688	1.932	-6.460; 1.047	
		Lockdown status * Year 2019	**-5.232**	**1.938**	**-9.077; -1.537**	
		Lockdown status * Year 2020	-3.673	1.988	-7.574; 0.150	
Blue tit	Lay date	(Intercept)	11.868	1.095	9.815; 13.956	
n = 251		*Year*				-
		Year 2018	**6.578**	**1.011**	**4.609; 8.536**	
Family: Gaussian		**Year 2019**	**3.000**	**1.066**	**0.905; 5.048**	
Random: Study site		**Year 2020**	**3.562**	**1.017**	**1.572; 5.523**	
		Lockdown status (LEA)	-1.192	1.591	-4.191; 1.790	-
		*Lockdown status * Year*				-

		Lockdown status * Year 2018	-0.674	1.702	-3.975; 2.635	
		Lockdown status * Year 2019	-0.349	1.902	-4.032; 3.351	
		Lockdown status * Year 2020	-1.175	1.778	-4.628; 2.272	

Species	**Response**	**Variable**	**Estimate**	**se**	**CI 95%**	**Relative importance**
Great tit	Clutch size	(Intercept)	8.813	0.556	7.723; 9.903	
n = 278		*Year*				1.00
		Year 2018	0.416	0.329	-0.229; 1.060	
Family: Gaussian		Year 2019	-0.291	0.311	-0.900; 0.318	
Random: Study site		**Year 2020**	**-0.599**	**0.303**	**-1.193; -0.004**	
		Lay date	**-0.043**	**0.015**	**-0.072; -0.014**	0.44
		Lockdown status (LEA)	-0.641	0.749	-2.108; 0.827	0.52
		*Lockdown status * Year*				0.14
		Lockdown status * Year 2018	0.540	0.487	-0.414; 1.495	
		Lockdown status * Year 2019	**1.063**	**0.490**	**0.103; 2.023**	
		Lockdown status * Year 2020	0.543	0.501	-0.440; 1.526	
Blue tit	Clutch size	(Intercept)	10.821	0.352	10.125; 11.513	
n = 245		**Lay date**	**-0.076**	**0.016**	**-0.107; -0.043**	-
Family: Gaussian						
Random: Study site						

Species	**Response**	**Variable**	**Estimate**	**se**	**CI 95%**	**Relative importance**
Great tit	Incubation duration	(Intercept)	15.947	0.624	14.724; 17.170	
n = 245		*Year*				1.00
		Year 2018	**-3.364**	**0.642**	**-4.622; -2.106**	
Family: Gaussian		**Year 2019**	**-2.509**	**0.589**	**-3.663; -1.355**	
		Year 2020	**-1.255**	**0.599**	**-2.428; -0.082**	
		Lay date	**-0.101**	**0.037**	**-0.174; -0.028**	1.00
		Lockdown status (LEA)	-0.517	0.385	-1.270; 0.237	0.47
Blue tit	Incubation duration	(Intercept)	15.759	0.419	14.937; 16.581	
n = 232		*Year*				1.00

	Year 2018	**-3.483**	**0.413**	**-4.293; -2.673**	
Family: Gaussian	**Year 2019**	**-3.060**	**0.404**	**-3.852; -2.268**	
	Year 2020	**-1.991**	**0.382**	**-2.741; -1.242**	
	Lay date	**-0.096**	**0.028**	**-0.150; -0.042**	1.00
	Lockdown status (LEA)	-0.366	0.298	-0.950; 0.218	0.43

Table 2. Model - averaged summary statistics of best fitting GLMs and LMMs testing the effect of lockdown restrictions on great tit and blue tit life - history trait variation.

Table 2. *(caption):* Model – averaged summary statistics of Generalised Linear Models (GLMs) and Linear Mixed Effects Models (LMMs) testing the association between lockdown and life – history traits in great tits and blue tits. The effect of “Lockdown status” is reported for “LEA” relative to “LENA” sites. “Year” effects are reported for each year relative to 2017. Details on model structures are specified in the methodological section 2.4.1. Parameters with confidence intervals not overlapping “0” are highlighted **in bold**. The symbol (*) indicates the interaction tested between “Year” and “Lockdown status” categories.

Species	Response	Variable	Estimate	se	CI 95%	Relative importance
Great tit	Occupancy	(Intercept)	-1.961	0.168	-2.291; -1.631	
n = 1636		*Year*				1.00
(1 = 294; 0 = 1342)		**Year 2018**	**0.510**	**0.190**	**0.137; 0.882**	
		Year 2019	**0.480**	**0.191**	**0.106; 0.853**	
Family: Binomial		Year 2020	0.336	0.194	-0.045; 0.717	
		Tree cover	0.004	0.002	0; 0.008	0.73
Blue tit	Occupancy	(Intercept)	-1.661	0.110	-1.877; -1.446	
n = 1636		*Year*				0.223
(1 = 251; 0 = 1385)		Year 2018	-0.070	0.187	-0.436; 0.297	
		Year 2019	-0.388	0.199	-0.778; 0.001	
Family: Binomial		Year 2020	-0.162	0.190	-0.534; 0.211	
		Tree cover	-0.002	0.002	-0.006; 0.003	0.258

Species	Response	Variable	Estimate	se	CI 95%	Relative importance
Great tit	Lay date	(Intercept)	11.478	0.843	9.826; 13.131	
n = 290		*Year*				1.00
Family: Gaussian		**Year 2018**	**7.926**	**0.954**	**6.055; 9.797**	
		Year 2019	**4.420**	**0.959**	**2.541; 6.299**	
		Year 2020	**6.078**	**0.979**	**4.159; 7.996**	
		Tree cover	0.015	0.011	-0.006; 0.037	0.49
Blue tit	Lay date	(Intercept)	9.872	0.682	8.536; 11.208	
n = 251		*Year*				-
Family: Gaussian		**Year 2018**	**6.327**	**0.825**	**4.710; 7.944**	
		Year 2019	**2.676**	**0.889**	**0.933; 4.418**	
		Year 2020	**3.176**	**0.842**	**1.525; 4.827**	
		Tree cover	**0.037**	**0.012**	**0.014; 0.061**	-

Species	Response	Variable	Estimate	se	CI 95%	Relative importance
Great tit	Clutch size	(Intercept)	8.238	0.357	7.538; 8.939	
n = 278		*Year*				1.00
Family: Gaussian		Year 2018	0.212	0.428	-0.626; 1.050	
		Year 2019	-0.209	0.356	-0.907; 0.489	
		Year 2020	-0.525	0.374	-1.258; 0.208	
		*Tree cover * Year*				0.48

		Tree cover * Year 2018	0.014	0.009	-0.004; 0.031	
		Tree cover * Year 2019	-0.005	0.009	-0.022; 0.013	
		Tree cover				
		Tree cover * Year 2020	-0.003	0.009	-0.021; 0.015	
		Tree cover	**0.017**	**0.005**	**0.007; 0.027**	
		Lay date	-0.030	0.017	-0.062; 0.003	0.64
Blue tit	Clutch size	(Intercept)	10.567	0.260	10.057; 11.078	
n = 245		*Year*				0.31
Family: Gaussian		Year 2018	-0.068	0.267	-0.590; 0.455	
		Year 2019	0.094	0.261	-0.418; 0.607	
		Year 2020	-0.425	0.250	-0.916; 0.066	
		Tree cover	**0.014**	**0.004**	**0.007; 0.021**	1.00
		Lay date	**-0.079**	**0.017**	**-0.113; -0.045**	1.00
Species	**Response**	**Variable**	**Estimate**	**se**	**CI 95%**	**Relative importance**
Great tit	Incubation duration	(Intercept)	15.830	0.631	14.593; 17.068	
		Year				1.00
n = 245		**Year 2018**	**-3.432**	**0.649**	**-4.705; -2.160**	
Family: Gaussian		**Year 2019**	**-2.557**	**0.593**	**-3.720; -1.394**	
		Year 2020	**-1.252**	**0.602**	**-2.433; -0.072**	
		Lay date	**-0.097**	**0.038**	**-0.171; -0.023**	1.00
		Tree cover	-0.008	0.007	-0.021; 0.005	0.42
Blue tit	Incubation duration	(Intercept)	15.686	0.399	14.905; 16.467	
n = 232		*Year*				-
Family: Gaussian		**Year 2018**	**-3.492**	**0.411**	**-4.297; -2.686**	
		Year 2019	**-3.046**	**0.402**	**-3.833; -2.259**	
		Year 2020	**-1.983**	**0.380**	**-2.728; -1.238**	
		Lay date	**-0.094**	**0.027**	**-0.148; -0.041**	-

Table 3. Model - averaged summary statistics of best fitting GLMs testing the effect of Tree cover and other covariates on great tit and blue tit life- history trait variation.

Table 3. Model – averaged summary statistics of Generalised Linear Models (GLMs) testing the association between tree cover (in %) and life – history traits in great tits and blue tits. “Year” effects were reported for each year relative to 2017. Details on model structures are specified in the methodological section 2.4.2. Parameters with confidence intervals not overlapping “0” are highlighted **in bold**. The symbol (*) indicates the interaction tested between “Year” and “Tree cover”.

FIGURES:

Figure 1. Study sites locations in the capital city of Warsaw, Poland.

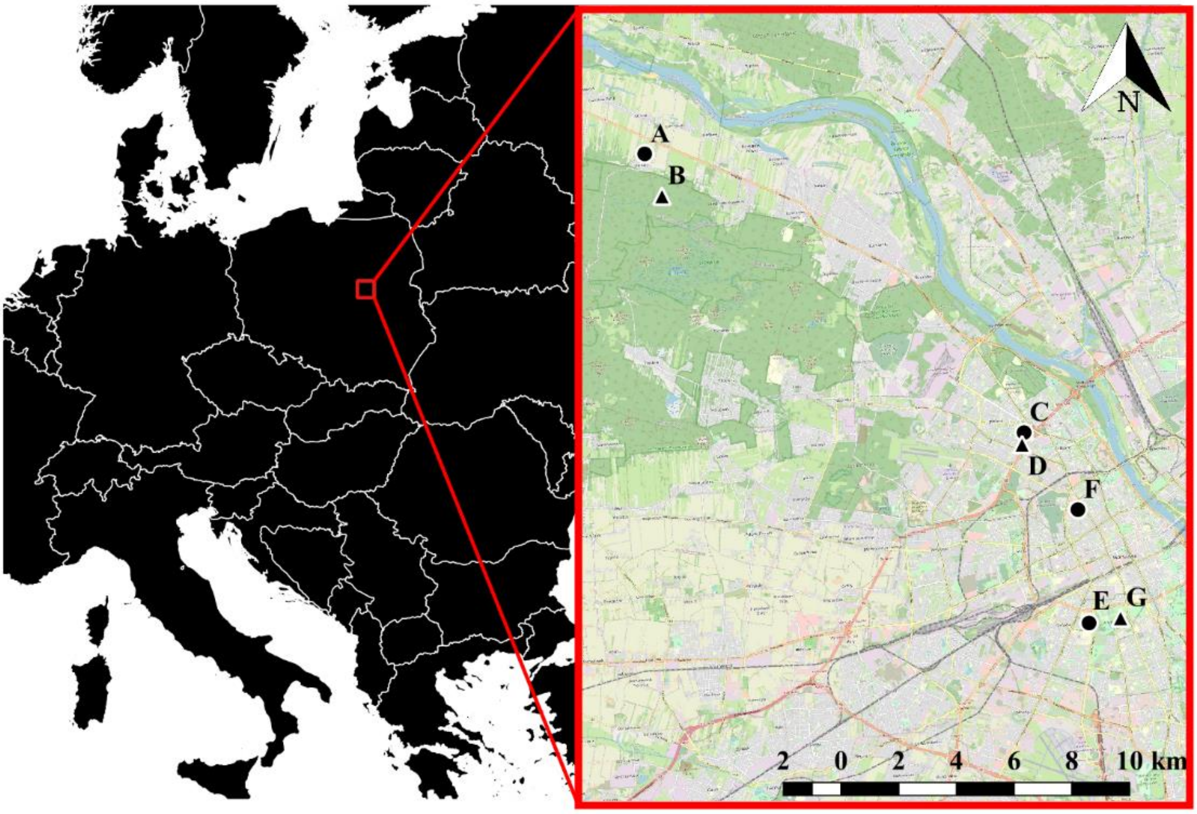

Figure 1. Map of sites locations in the Warsaw gradient of urbanisation, Poland. These include: a suburban village (A), a natural forest (B), two residential areas (C and F), an urban woodland (D), an office area (E), and an urban park (G). Dots and triangles indicate whether study sites were categorised as "Lockdown – Entrance Allowed (LEA)" or "Lockdown – Entrance Not Allowed (LENA)" sites during the 2020 SARS-CoV-2 pandemic.

Figure 2. Great tit and blue tit life-history traits: a comparison between “Lockdown - Entrance Allowed” (LEA) and “Lockdown-Entrance Not Allowed” (LENA) sites across four years of investigation.

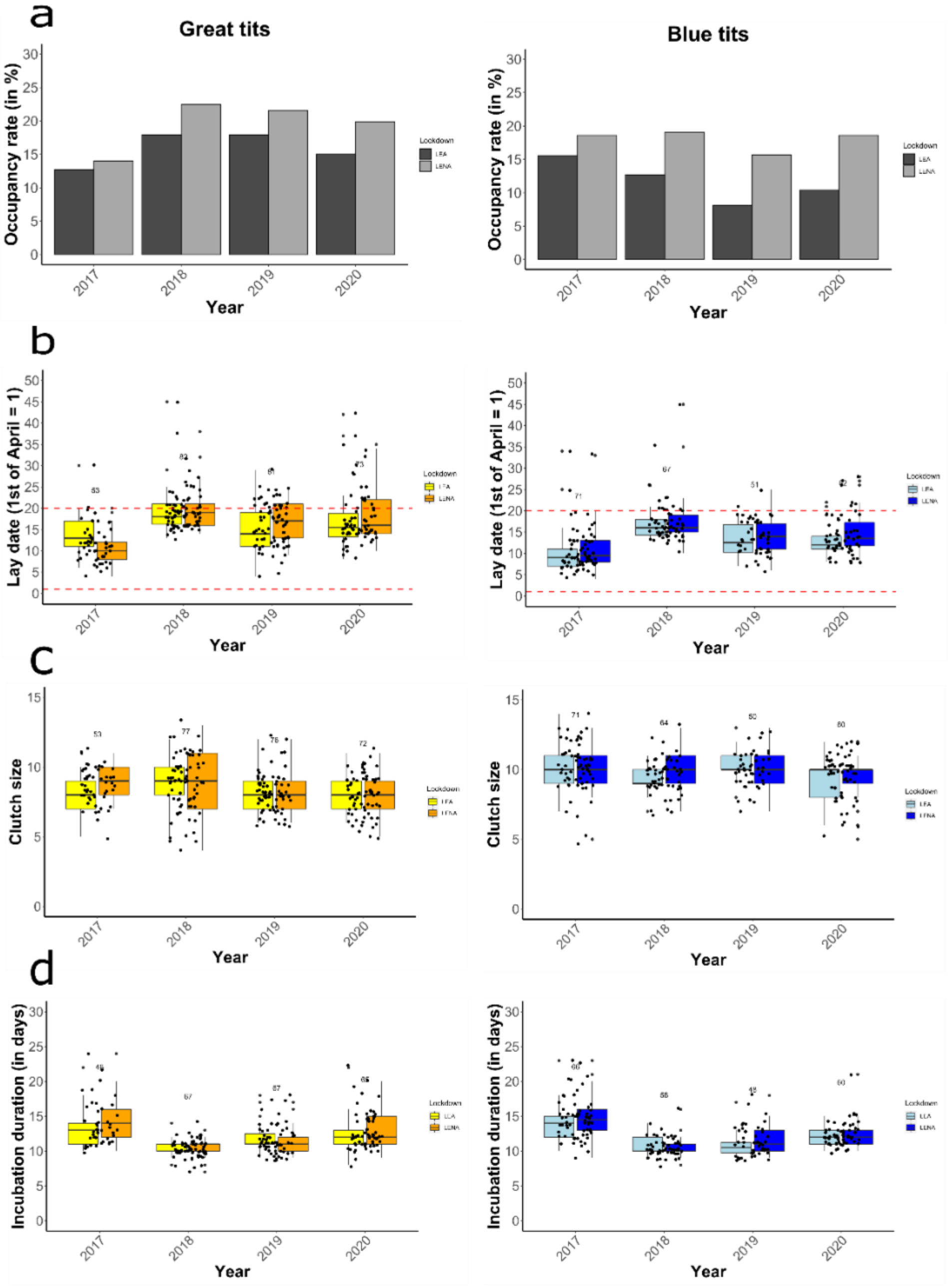
a
Great tits
Blue tits
Occupancy rate (in %)
Year
2017
2018
2019
2020
Lockdown
LEA
LENA
b
Lay date (1st of April = 1)
c
Clutch size
d
Incubation duration (in days)

Figure 2. Great tit (left) and blue tit (right) life-history traits comparisons between "Lockdown – Entrance Allowed" (LEA) and "Lockdown – Entrance Not Allowed" (LENA) sites across the four years. No significant differences between LEA and LENA sites were reported in terms of nestboxes occupancy (a), lay date (b), clutch size (c) and incubation duration (d) in both species. In (b), the red-dashed line indicates the duration of lockdown restrictions implemented in Poland [from the 1st of April until the 20th of April 2020].

Figure 3. Positive association between tree cover and clutch size in great tits and blue tits

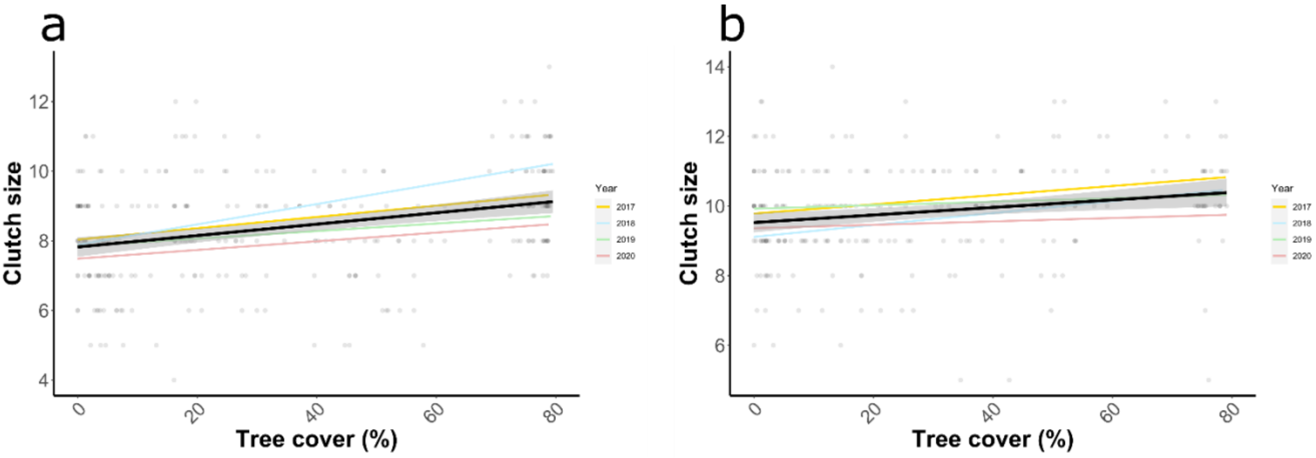

Figure 3. Linear regression plots reporting the original relationship between clutch size and the extent of tree cover in a 100m radius surrounding the nestbox in (a) great tits and (b) blue tits. Full models confirming the significant relationship between the two variables are reported in Table 3.

Supplementary Information

Breeding in the pandemic: short-term lockdown restrictions do not alter reproductive decisions and avian life-history traits in a European capital city

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Abstract

Humans are transforming natural habitats into managed urban green areas and impervious surfaces with unprecedented pace. Yet the effects of human presence *per se* on animal life-history traits are rarely tested. This is particularly true in cities, where human presence is often indissociable from urbanisation itself. The onset of the SARS-CoV-2 outbreak, along with the resulting lockdown restrictions, offered a unique, “natural experiment” context to investigate wildlife responses to a sudden reduction of human activities. We analysed four years of avian breeding data collected in a European capital city to test whether lockdown measures altered nestbox occupancy and life-history traits in two urban adapters: great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*). Lockdown measures, which modulated human presence, did not influence any of the life-history traits inferred. In contrast, tree cover, a distinct ecological attribute of the urban space, positively influenced clutch size, a key avian life-history and reproductive trait. This highlights the importance of habitat and food webs over human activity on animal reproduction in cities. We discuss our results in the light of other urban wildlife studies carried

out during the pandemic, inviting the scientific community to carefully interpret all lockdown - associated shifts in biological traits.

Table S1. Subset of GLMs and LMMs ($\Delta AIC_c < 2$) with binomial and Gaussian distribution testing the association between lockdown restrictions and avian breeding occupancy and life – history traits.

Occupancy rate – binomial distribution – Lockdown categories				
Species	**Model subset**	**AIC_c**	**ΔAIC_c**	**AIC_c weight**
Great tit n = 1636 1 = 294; 0 = 1342 Family: binomial	(Intercept) + Lockdown status + Year	1538.4	0.0	0.684
	(Intercept) + Year	1539.9	1.54	0.316
Blue tit n = 1636 1 = 251; 0 = 1385 Family: binomial	(Intercept) + Lockdown status	1393.9	0.0	0.697
	(Intercept) + Lockdownvstatus + Year	1395.5	1.67	0.303
Laying date – Gaussian distribution – Lockdown categories				
Species	**Model subset**	**AIC_c**	**ΔAIC_c**	**AIC_c weight**
Great tit n = 290 Family: Gaussian	(Intercept) + Year + Lockdown status + Lockdown status * Year	1795.1	0	1
Blue tit n = 251 Family: Gaussian	(Intercept) + Year + Lockdown status + Lockdown status * Year	1502.1	0	1
Clutch size – Gaussian distribution – Lockdown categories				
Species	**Model subset**	**AIC_c**	**ΔAIC_c**	**AIC_c weight**
Great tit n = 278 Family: Gaussian	(Intercept) + Year	974.3	0.0	0.538
	(Intercept) + Year + Lay date	974.6	0.3	0.462
Blue tit n = 245 Family: Gaussian	(Intercept) + Lay date	866.7	0	1
Incubation duration – Gaussian distribution - Lockdown categories				
Species	**Model subset**	**AIC_c**	**ΔAIC_c**	**AIC_c weight**
Great tit n = 245 Family: Gaussian	(Intercept) +_ Year + Lay date	1226.4	0.0	0.534
	(Intercept) + Year + Lay date + Lockdown status	1226.7	0.28	0.466
Blue tit n = 232 Family: Gaussian	(Intercept) + Year + Lay date	1006.7	0.0	0.57
	(Intercept) + Year + Lay date + Lockdown status	1007.3	0.57	0.43

Table S1. Subset of Generalised Linear Models and Linear Mixed Effects Models with binomial and Gaussian distribution partitioning variation in great tit and blue tit breeding occupancy and life-history traits ($\Delta AIC_c < 2$). Data were collected for four years (from 2017 to 2020), models were run for great tits and blue tits separately. Model structures are described in section 2.4.1.

Table S2. Subset of GLMs (ΔAIC$_c$ < 2) with binomial and Gaussian distribution testing the association between tree cover (in %) and avian breeding occupancy and life-history traits.

Occupancy rate - % Tree cover				
Species	**Model subset**	**AIC$_c$**	**ΔAIC$_c$**	**AIC$_c$ weight**
Great tit n = 1636 1 = 294; 0 = 1342 Family: binomial	(Intercept) + Tree cover + Year	1537.9	0.0	0.73
	(Intercept) + Year	1539.9	1.99	0.27
Blue tit n = 1636 1 = 251; 0 = 1385 Family: binomial	(Intercept)	1404.4	0.0	0.519
	(Intercept) + Tree cover	1405.8	1.40	0.258
	(Intercept) + Year	1406.1	1.69	0.223
Laying date - % Tree cover				
Species	**Model subset**	**AIC$_c$**	**ΔAIC$_c$**	**AIC$_c$ weight**
Great tit n = 290 Family: Gaussian	(Intercept) + Year	1807.8	0.0	0.506
	(Intercept) + Year + Tree cover	1807.8	0.05	0.494
Blue tit n = 251 Family: Gaussian	(Intercept) + Year + Tree cover	1511.5	0.0	1
Clutch size - % Tree cover				
Species	**Model subset**	**AIC$_c$**	**ΔAIC$_c$**	**AIC$_c$ weight**
Great tit n = 278 Family: Gaussian	(Intercept) + Year + Tree cover + Lay date	1010.3	0.0	0.334
	(Intercept) + Year + Tree cover + Lay date + Tree cover * Year	1010.5	0.17	0.307
Blue tit n = 245 Family: Gaussian	(Intercept) + Tree cover + Lay date	861.1	0.0	0.687
	(Intercept) + Year + Tree cover + Lay date	862.7	1.57	0.313
Incubation duration - % Tree cover				
Species	**Model subset**	**AIC$_c$**	**ΔAIC$_c$**	**AIC$_c$ weight**
Great tit n = 245 Family: Gaussian	(Intercept) + Year + Lay date	1226.4	0.0	0.581
	(Intercept) + Year + Tree cover + Lay date	1227.1	0.66	0.419
Blue tit n = 232 Family: Gaussian	(Intercept) + Year + Lay date	1006.7	0.0	1

Table S2. Subset of Generalised Linear Models with binomial and Gaussian distribution partitioning great tit and blue tit variation in breeding occupancy and life-history traits (ΔAIC$_c$ < 2). Data were collected for four years (from 2017 to 2020), models were run for great tits and blue tits. Model structures are described in section 2.4.2.

Table S3. Summary statistics of percentage tree cover in nestboxes occupied by great tits and blue tits from 2017 to 2020. For the entire dataset (n=409 nestboxes), the overall average tree cover (mean ± se) was 6.6% (± 0.64) and 49.1% (± 1.84) in LEA (n = 173) and LENA (n = 236) study sites, respectively.

Species	Year	n	Mean (± se)
Great tit	2017	53	36.1 (± 4.2)
	2018	84	31.8 (± 3.1)
	2019	81	32.7 (± 3.3)
	2020	73	38.4 (± 3.4)
Blue tit	2017	71	30.3 (± 3.0)
	2018	67	30.3 (± 3.1)
	2019	51	30.6 (± 3.6)
	2020	62	27.7 (± 3.3)

Table S3. Average tree cover in a 100m radius around each nestbox: "n" refers to the number of occupied nests within each year. Only first broods were included in the table. LEA stands for "Lockdown – Entrance Allowed", LENA stands for "Lockdown – Entrance Not Allowed"

Table S4. Z-tests for equality of proportions of occupied nestboxes in LEA and LENA study sites by year.

Species	Year	N_{LEA}	N_{LENA}	χ^2	DF	p-value
Great tit	2017	22	33	0.050	1	0.8
	2018	31	53	0.997	1	0.3
	2019	31	51	0.634	1	0.4
	2020	26	47	1.309	1	0.2
Blue tit	2017	27	44	0.447	1	0.5
	2018	22	45	2.494	1	0.1
	2019	14	37	**4.590**	**1**	**0.03**
	2020	18	44	**4.648**	**1**	**0.03**

Table S4. The total number of nestboxes available in LEA and LENA study sites was 173 and 236, respectively. N_{LEA} and N_{LENA} refers to the total number of nestboxes occupied within each lockdown status category.

Table S5. No *year* effects in tree-cover variation among occupied nestboxes.

Great tit

	Df	**Sum sq**	**Mean sq**	**F**	**p**
Year	3	2111	703.8	0.824	0.481
Residuals	287	244992	853.6		

Blue tit

	Df	**Sum sq**	**Mean sq**	**F**	**p**
Year	3	333	111.1	0.171	0.916
Residuals	247	160338	649.1		