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Avian behaviour changes in response to human activity during the COVID-19 lockdown in the United Kingdom

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Human activities may impact animal habitat and resource use, potentially influencing contemporary evolution in animals. In the United Kingdom, COVID-19 lockdown restrictions resulted in sudden, drastic alterations to human activity. We hypothesized that short-term daily and long-term seasonal changes in human mobility might result in changes in bird habitat use, depending on the mobility type (home, parks and grocery) and extent of change. Using Google human mobility data and 872 850 bird observations, we determined that during lockdown, human mobility changes resulted in altered habitat use in 80% (20/25) of our focal bird species. When humans spent more time at home, over half of affected species had lower counts, perhaps resulting from the disturbance of birds in garden habitats. Bird counts of some species (e.g. rooks and gulls) increased over the short term as humans spent more time at parks, possibly due to human-sourced food resources (e.g. picnic refuse), while counts of other species (e.g. tits and sparrows) decreased. All affected species increased counts when humans spent less time at grocery services. Avian species rapidly adjusted to the novel environmental conditions and demonstrated behavioural plasticity, but with diverse responses, reflecting the different interactions and pressures caused by human activity.

1. Introduction

Humans are a driving force behind contemporary evolution, altering animal habitat and resource use as a result of many ecological impacts, such as hunting, agriculture, urbanization and biological invasions [1]. In recent centuries, human activity and mobility have increased exponentially, often negatively impacting natural areas and wildlife and leading to complex changes in species traits and community structure [2]. As these human-induced changes are on a larger spatial scale and/or have occurred at a faster rate than other forms of natural environmental variation, they are referred to as human-induced rapid environmental change (HIREC) and represent a key contemporary driver of evolution [3].

Anthropogenic factors may contribute towards the evolution of species' traits, including behavioural traits related to resource use [4,5]. For example, animals living in urban habitats tend to have high rates of feeding innovation that enable them to exploit novel food resources [4], which then may increase their survival and fitness. For many species, behavioural adjustments represent the first response to HIREC. Therefore, behavioural plasticity may allow species to adjust to rapid anthropogenic changes and may explain why some species are able to survive under HIREC conditions, while other species do not [5,6]. For example, some species have shifted their foraging behaviours to avoid humans and vehicles [7], while others avoid breeding in areas of heavy human use [8]. Often as a result of relatively high behavioural plasticity, some species have adapted their behaviours to human-altered landscapes successfully and can live and reproduce in cities and areas of dense human occupation [4].

Behavioural change may lead to further evolutionary changes as a result of eco-evolutionary feedbacks because ecological changes may result in behavioural responses that impact evolutionary processes directly or may cause further evolutionary changes in behaviour [5,6]. For example, some species have changed the timing and duration of their breeding patterns in response to year-round human-provisioned food resources [4]. Thus, dramatic changes in human activity or behaviour, which may alter behavioural responses, may provide an opportunity to examine human-influenced mechanisms involved in the eco-evolutionary processes influencing animal behaviour.

In the United Kingdom (UK), there is a long historical relationship between birds coexisting with dense human populations [9]. Land in the UK has been heavily modified by human development for centuries, and as a result, the UK has seen massive losses in wilderness areas and biodiversity [10]. Therefore, the evolution of many avian species in the UK has been influenced by human activity, and some species have adapted to, and even become dependent on, human-modified habitats and human-sourced resources [10,11]. By contrast, other British avian species have declined as a result of human activity [10]. These anthropogenic habitat alterations have often favoured generalist over specialist species [12]. In the UK, avian communities have become less specialized over time [13], indicating that the evolution of avian species and communities has probably been influenced by human activity. While the exact mechanisms behind these changes remain unclear [12], it seems likely that these species-specific and community-level changes have resulted in populations of species that are more tolerant of human activity than those in geographic locations with more natural habitat in which birds could avoid humans and thus the need to adapt to human-modified environments.

In 2020, the COVID-19 pandemic resulted in unprecedented changes to worldwide human activity. In March 2020, severe lockdown restrictions confining humans largely to their homes came into effect in the UK, drastically altering human activity. Some types of human activity, such as air and ground vehicular traffic, decreased [14], while the use of recreational areas increased in some locations [15]. As a result, human movement restrictions during the pandemic changed the availability of undisturbed habitat [15,16], altered the availability of human-sourced resources [17,18], decreased wildlife mortality caused by vehicular and aircraft collision [19–23], modified predator presence [24,25] and altered human hunting pressure [26]. Some of these human-induced patterns have influenced species' behaviours [17,18,27–30]. Surprisingly, however, wildlife showed both increased and decreased use of different habitat types, including habitats with varying degrees of human activity, during the pandemic [30,31], thus demonstrating the complex influence of human activity on animal behaviour. Where wildlife had previously adapted to and benefited from human activities, such as species that use human-sourced food resources, or where wildlife protection and conservation management initiatives have suddenly ceased [14,31], wildlife faced new challenges to survival during COVID-19 lockdowns.

Even though studies have examined characteristics of species that are tolerant of human activity (e.g. [4,31]), the traits that have been identified as being associated with species that live in close association with human activity [32] or cope well with HIREC (e.g. behaviourally plastic, innovative and exploratory) have by necessity been primarily identified based on observational studies. Therefore, the mechanisms behind evolution of these adaptive traits are poorly understood [4]. Lockdown restrictions created an unprecedented immediate and dramatic environmental change to which species may or may not respond to, creating a mensurative experiment that allowed for examining prior hypotheses of which traits are associated with species that cope well with HIREC. Comparing the response of species that share phenotypic characteristics or evolutionary history, in response to different types of human activity changes, may help us understand the mechanisms behind the adjustment of species to HIREC.

In the UK, during the COVID-19 lockdown, which coincided with the UK bird migration and breeding season (April–July), birds experienced many unusual ecological conditions resulting from drastic changes in human behaviour. During lockdowns, human activities in homes and backyard gardens increased, with decreased vehicular travel to other locations, such as retail and grocery locations, which may have consequently decreased vehicular traffic animal mortality [19–22], pollution and noise disturbance [28,33,34], and roadkill carrion resources [19–22]. Also, when humans stayed at home more, species dependent on gardens may have faced increases in human disturbance, while perhaps benefitting from increased food provisioning during lockdown [35], when humans were more attentive to their home environments including bird feeders. During UK lockdowns, although human activities in parks increased in some regions or at particular park types (e.g. natural beauty spots that remained opened during lockdown, [36,37]), parks in other regions or other park types (e.g. parks associated with trusts that closed during the pandemic, electronic supplementary material, table S1) saw decreases in human activity. Increased use of parks and recreational areas may have increased disturbance to species dependent on parks while providing human-sourced food resources (e.g. picnic refuse); presumably, decreased human activity in parks had the reverse result [16,38]. Furthermore, the lockdown severity, and thus changes in human mobility, varied by region [14,31]; some UK regions saw greater changes in the use of home, parks and grocery locations compared to other areas.

As bird abundance can be affected by human presence and activity [38], we evaluated whether changes in different types of human mobility patterns as a result of COVID-19 restrictions affected counts of 25 avian species across a wide range of habitat types. Exploring whether the number of birds seen during the first pandemic lockdown differed from those recorded prior to lockdowns, and evaluating whether bird counts changed more on days and in regions with greater changes relative to various indices of human mobility (time spent at home, parks and grocery) allowed us to examine the relationships between habitat type (e.g. garden feeder species), resource use (e.g. food source), body size, evolutionary history (i.e. taxonomic family) and avian species' responses to rapid changes in human activity.

We hypothesized that if altered bird detections resulted from changes in human mobility, changes in bird counts should be greater on days with greater changes in mobility (daily mobility) and in regions with greater changes in human mobility over the long term (seasonal mobility). Also, we hypothesized that species' response to changes in human mobility would be influenced by the trade-off between the use of food resources and minimizing disturbance. Specifically, given that species vary in their food resources and the extent of use of human-sourced food sources [11] and may make trade-offs between the threats from human disturbance versus the benefits of human-sourced food resources [39], we predicted that changes in bird counts (i.e. increase, decrease and no change) during the pandemic, in comparison to bird counts taken during pre-pandemic time periods, would depend on the species' habitat type, and the type of food resource that is used (i.e. human-sourced food, nature-sourced foods). For example, species such as blue tits, which heavily use garden feeders, would be predicted to have greater changes in bird counts in response to changes in human mobility at home, compared to changes in human mobility at essential retail services. Species that feed on human food refuse, such as gulls, would be predicted to decrease in counts as humans spent more time at home, and increase in counts when human spent more time at parks (which may be associated with picnicking). Carrion eaters, such as corvids, would be predicted to decrease in counts as humans spent more time at home and increase in counts when human drove more (i.e. spent more time at parks and essential retail services). Additionally, as tolerance to humans varies among species [40] and is influenced by species' traits [11,41,42] with larger species often being more tolerant to human disturbance [41], we predicted that smaller bodied species will have been more likely to change bird counts in response to human mobility changes, compared to larger species. Furthermore, as different species can respond to human impacts in different ways that allow them to cope with disturbance and/or benefit from anthropogenic resources [4], but responses may likely be similar in related species [43], we predicted that closely related species (within families) would have similar responses to changes in human activity.

2. Methods

We examined the effects of human mobility on bird species in the UK from 1 March to 4 July 2020 (18 weeks), which coincides with the UK avian breeding season. Our study period encompassed several time periods associated with changes in human mobility, including (i) the time leading up to government-mandated nation-wide lockdown (1–22 March 2020), as humans started responding to the threat of the pandemic with mobility changes; (ii) strict government-mandated lockdown travel restrictions starting on 23 March 2020 and (iii) the first phase of lockdown easing in mid-June (with dates of lockdown easing varying among different regions of the UK). We compared bird counts during our study period in 2020 (during pandemic) to counts during the same period in the previous three breeding seasons (pre-pandemic, 1 March–4 July; 2017, 2018 and 2019).

The study area encompassed all of the UK and was separated into individual regions ($n = 383$; electronic supplementary material, table S2), as defined by the classification of administrative councils by Google Mobility [44], hereafter referred to as 'district'. To ensure we had sufficient data to examine changes in bird counts across the 18 weeks of study and among regions, our focal species included the most recorded 25 bird species on eBird checklists in the UK (electronic supplementary material, tables S3 and S4); we note that these species might not be the most common avian species in the UK (see [45]). Our 25 focal species included a variety of common garden, woodland and urban bird species, which vary in size and the extent that they occupy human-dominated habitats ([11,36,43]; electronic supplementary material, table S3). For each of our focal species, we examined 34 914 checklists sourced from geographical locations across the whole of the UK.

(a) Data sources and data processing

(i) Human mobility

To evaluate relative changes in human mobility among regions (districts) and relative to different location types (home, parks and essential retail services), and to quantify changes in human mobility across time periods (daily short-term versus long-term seasonal changes), we obtained data online from the publicly available *Google Covid-19 community mobility reports* [44], which used the movement of mobile phones to estimate relative changes in human mobility across time and space. These data are reported as the 'percentage change from baseline' where the pre-pandemic baseline is the median mobility value for the corresponding day of the week, calculated over a five-week period (3 Jan–6 Feb 2020). Ideally, we would have liked to compare changes in human mobility in 2020 to mobility in 2019, for the same dates of this study (1 March–4 July), to control for seasonal changes in behaviour. However, these data were not available. We concluded that the Google Mobility data were the best available index of changes in human behaviour during the pandemic and follow the lead of other studies that have used these data for this purpose (e.g. [30]), because, (i) they are the only data available that break down changes in human behaviour by district, (ii) we used them to assess the impact of immediate changes in human behaviour relative to what birds would have been experiencing at the current time in the absence of lockdowns (relative changes in human behaviour) and (iii) the altered human behaviour documented by these data demonstrate extraordinary changes immediately following lockdowns that seem to be best explained by responses to the pandemic (figure 1).

Google Mobility reported data for each district and relative to change in activity levels in different human land-use types: (i) residential areas, defined as all places of residence (hereafter referred to as 'home'); (ii) park areas (parks) defined as local parks, national parks, public beaches, marinas, dog parks, plazas and public gardens; (iii) grocery and pharmacy (i.e. essential retail places; 'grocery'), defined as grocery markets, food warehouses, farmers markets, speciality food shops, drug stores and pharmacies; (iv) workplaces; (v) retail and recreation, defined as restaurants, cafes, shopping centres, theme parks, museums, libraries and movie theatres; and (vi) transit stations as defined as public transport hubs such as subway, bus and train stations [44].

We evaluated whether time spent at home, parks and grocery changed during the pandemic in comparison with the baseline period. Unsurprisingly, time spent at home was strongly negatively correlated with time spent at work, non-essential retail services, and at transit stops ($r \geq -0.97$), and as such, home was a useful proxy for indicating change in human mobility relative to all those locations. We used three separate models for examining daily mobility changes at home, parks and grocery locations. We modelled the daily percentage mobility change from baseline as a function of the covariate 'date', using a Gaussian error distribution. We also incorporated the dependency among observations of the same district by including district as a random intercept.

Next, we evaluated whether observations of birds (hereafter, bird counts) changed as human time spent at home, in parks or at grocery locations changed. Additionally, we assessed impacts of lockdowns at two temporal scales, as both bird and human behaviour vary both daily and over the course of a breeding season. Birds select from their local habitats at a minute-to-minute or daily temporal scale to avoid risky locations or select for resource-rich habitats. However, birds are also constrained by the ecological conditions in the district where they are living, such as the nest location that they commit to early in the breeding season, territory locations, and species-specific and individual behavioural traits such as dispersal abilities [46], so they may have different habitat selection strategies over the short and long terms. Changes in human mobility are also predicted to have different impacts at different scales. In the short term, increased time spent gardening

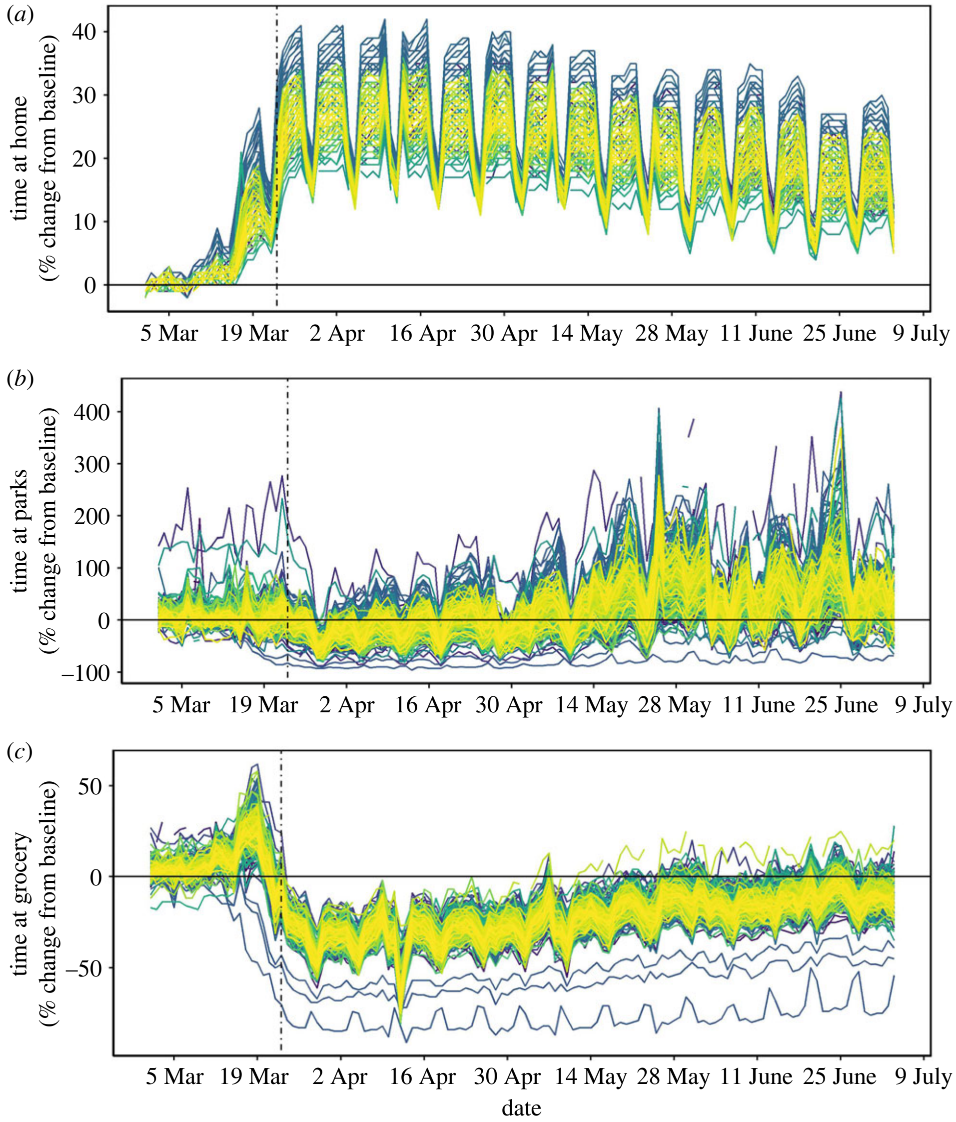

Figure 1. Percentage change from baseline in daily human mobility (one line for each region) in the UK from 1 March to 4 July 2020. Vertical dashed line marks the first day of lockdown on 23 March 2020. Time spent at home/parks/grocery (*a–c*) (*y*-axis) was calculated by Google LLC (2020). (Online version in colour.)

at home, for example, might flush or displace birds from resource-rich residential gardens, potentially temporarily decreasing counts of species sensitive to human disturbance. However, over the course of the first lockdown, decreased traffic may have made some habitats more suitable for species that are sensitive to noise or road mortality (see also [30]). We thus first evaluated correlations between *daily* changes in human mobility within districts and daily detections of birds reported through eBird. Second, we compared long-term *seasonal* changes in human mobility across the whole breeding season (the entire 18 weeks of the study), which varied significantly among districts (figure 1). We thus measured each human mobility variable (home, parks and grocery) at both daily and seasonal temporal scales, such that we examined six human mobility variables (see model details below).

Bird populations fluctuate annually and geographically, regardless of lockdowns. To control for variation in birds among years and among districts, we focused our interpretation of the impacts of lockdowns on statistical *interactions* between year (pre-pandemic compared with during pandemic) and the degree of changes in mobility in each district. This allowed us to evaluate whether bird counts *changed more* in districts with larger changes in human mobility, or on days with greater changes in mobility. To do this, for the long-term seasonal temporal analysis, we calculated the average of the daily assigned values for changes in mobility to each district in the UK for both the pre-pandemic period and the during pandemic period. Daily changes in mobility indicate the difference between mobility within each district on each day of March–June 2020, in comparison with the baseline period in the same district. These values are meaningless in the 2017–2019 period and were simply used to determine whether there was a spurious correlation between future changes in mobility and characteristics of each district. Non-zero trends in data from the pre-pandemic period do not indicate an effect of the pandemic but instead reflects other variation among districts. The fact that we did detect non-zero trends in data collected during the pre-pandemic period—which could not have been caused by the pandemic, as it had not yet happened when the data were collected—confirmed both that (unsurprisingly) bird populations vary among districts, and that this variation needed to be accounted for in our analyses. The *interaction* comparison between the trends in 2020 (which reflect genuine changes in mobility) with the pre-pandemic period allowed us to account for these trends that are unrelated to pandemic lockdowns. At the long-term seasonal scale, changes in mobility indicate the difference between mobility among districts relative to the baseline period, such that a larger change in mobility indicated that human activity changed more in that district compared with other districts over the whole first lockdown. A significant interaction indicated that the change in detections of birds varied among districts differently during the lockdown than it did in the pre-pandemic period.

To distinguish between the effects of the degree of change in human mobility on a short-term daily basis, from typical changes in bird detections as seasons progress, we used a similar process to the one described above. Again, we focused on the *interaction* between year (pre- or during the pandemic) and degree of change in mobility on each day. To conduct this analysis to assess impacts of daily changes in mobility, the change in mobility for the during pandemic period was assigned as the degree of change in mobility for each district as provided by the Google Mobility data. We also assigned that change in mobility to that same day for the pre-pandemic period, essentially creating an index of 'the change in human mobility that will be experienced in the future'. For example, if mobility was 35% lower than the baseline on 27 July 2020, then we assigned that change in mobility to 27 July 2017, 2018 and 2019. Of course, this value is thus meaningless in the pre-pandemic period, so if a pattern emerged in the pre-pandemic period, that suggests that the observed spurious pattern was caused by something other than the pandemic, such as variation in detectability of birds, or changes in human behaviour. As we did observe some trends in the pre-pandemic period relative to 'future changes in mobility' (i.e. for the slopes based on data from 2017, 2018 and 2019), this again confirmed both that bird detections varied, and that this variation needed to be accounted for in our analyses. A significant *interaction* between daily changes in mobility and the pre-pandemic or during pandemic period indicated that the change in detections of birds varied among days (Julian days of the year) differently during the lockdown than it did in the pre-pandemic period.

(ii) Bird counts

We obtained avian count data from the community science program eBird, using the September 2020 version of the eBird Basic Dataset (eBird 2020). Each survey (termed a 'checklist') contained data on the number of each bird species, date, location and effort-related data such as the length of time and distance travelled. We used the 'auk' R package [47] to filter the database to only include checklists from 1 March–4 July 2017–2020. To be consistent with best practices recommended for using eBird data [48], we removed checklists that were not marked as 'complete' (i.e. observers had not recorded all birds that were detected), were not collected using either the 'stationary' or 'travelling' protocol, were longer than 5 h in duration, involved a distance travelled of greater than 5 km, had greater than 10 observers or were duplicate copies of shared checklists. Additionally, we removed checklists from a single user who contributed tens of thousands of checklists from a single region (orders of magnitude more than any other observer), so as not to bias the analysis to this region or individual.

Individuals contributing eBird checklist data (hereafter, 'users') may have changed their own birding behaviours during lockdowns relative to pre-lockdowns, and thus the geographic distribution of eBird effort may have been altered during the pandemic [49,50]. Therefore, we designed our analysis to reduce potential biases associated with changes in birding effort in different bird observation locations. First, as users tended to spend longer collecting checklists during the pandemic [50], we included both the distance travelled and duration of each checklist as covariates in the statistical model. Second, because users generally spent more time in urban and developed areas during lockdowns [50], we ensured that the spatial locations of checklists were the same in both pre-pandemic and pandemic periods by subsampling checklists across the landscape. We first imposed a system of hexagonal grid cells to cover the entire UK, with cell centres separated by three kilometres, and then we randomly selected an equal number of pre-pandemic (2017–2019) and pandemic (2020) checklists from each cell (*sensu* 12). Count data for each focal species were then extracted from each checklist in our subsamples. This process ensured that the spatial locations of checklists were the same in both pre-pandemic and pandemic periods at the 3 km scale. As it is unlikely that avian population sizes changed detectably during the relatively brief 18 weeks covered by the study, and we accounted for observer effort and location in the pre-pandemic and pandemic periods, we interpreted changes in birds counts between these time periods to indicate increased or decreased avian use of the areas being sampled (i.e. changes to behaviour, rather than population sizes).

(b) Statistical analysis

We used generalized linear mixed models, using R packages 'glmmTMB' [51] and 'MuMIn' [52] to examine the effects of human mobility changes (time spent at home, in park, and at grocery) on bird counts. For each of our 25 focal species, our response variable was the number of birds reported per checklist. The focus of our analyses was on interactions between the time period *Pandemic* ('prior to' or 'during' the pandemic) and six variables that described changes in human mobility (described below). Because we expected populations to differ among years, we did not evaluate whether the main effect of *Pandemic* was significant, but only assessed whether there were significant interactions between *Pandemic* and the human mobility variables. A significant effect of the interaction variable indicated that larger changes in human mobility resulted in increased impacts on observations of birds.

We used separate models for each of the 25 focal bird species in our study. To model the number of counts as a function of the covariates, we used a negative binomial error distribution (quadratic parameterization) with a log link function. The log link function ensures positive fitted values, and the negative binomial distribution generally fit longitudinal count data. Each model included 15 fixed covariates as follows:

(i–iii) *Short-term daily home/parks/grocery* (continuous): the percentage change from baseline in time spent at home/parks/grocery calculated for the date and district of each checklist. (iv–vi) *Long-term seasonal home/parks/grocery* (continuous): the percentage change from baseline in time spent at home/parks/grocery, calculated as the average daily mobility change for each district over the duration of the 18-week study. (vii) *Observer duration effort* (continuous): checklist duration (minutes). (viii) *Observer distance effort* (continuous): checklist distance (km). (ix) *Pandemic* (categorical with two levels): time period 'prior to' (2017, 2018 and 2019) or 'during' (2020) the pandemic. (x–xv): Interaction terms between the *pandemic* variable and variables 1–6. Correlation between covariates was low (typically below $+/-0.5$, with the largest correlation as -0.70). To incorporate the dependency among observations of the same district, we included *district* as a random intercept.

We examined qqplots and histograms of residuals with 'DHARMa' [53] to confirm good model fit and evaluated the significance of the fixed variables using the Wald Z statistics and p-values calculated from the conditional model [51]. We also used AIC as an index of goodness of fit, by comparing the full model with a model excluding the human mobility variables. Adding the human mobility variables improved model fit by 16 361 ± 1105 ΔAIC units.

(c) Detectability

While our mixed-effect models controlled for differences in human observer effort and survey locations, we could not control for all potential sources of detectability. During the pandemic lockdowns, noise pollution was reduced in urban areas [28,29,54], and this may have affected the ability of observers to detect some species [29,55]. If decreased traffic during the pandemic resulted in more birds being detected and counted, then we would expect that species whose detectabilities were negatively influenced by roads [56] would have shown increases in counts during the pandemic, compared to species whose detectabilities were not influenced by roads. Therefore, using detectability estimates from a previous study examining the effects of road exposure on detectability of UK birds [56], we examined the relationship between bird count changes (our study) and detectability changes associated with roads [56].

3. Results

(a) Human mobility

Human mobility significantly changed from 1 March to 4 July 2020, which included the time period leading up to lockdown (1–22 March 2020) and the first pandemic lockdown that officially started on 23 March 2020 (figure 1; electronic supplementary material, table S5). During lockdown, humans spent more time at home (daily % change from baseline mean(s.e.) = 17.6% ± 0.04%, $\beta[s.e.] = 0.07[0.001]$, $Z_{43403} = 60.1$, $p < 0.0001$) and parks (mean(s.e.) = 14.7% ± 0.22%, $\beta[s.e.] = 0.54[0.005]$, $Z_{44062} = 112.4$, $p < 0.0001$) and less time at grocery locations (mean(s.e.) = −16.8% ± 0.07%, $\beta[s.e.] = -0.06[0.002]$, $Z_{52172} = -30.92$, $p < 0.0001$).

Mobility changes also varied among districts with average within-district mobility changes ranging from +1% to +26% (homes), −73% to +146% (parks) and −67% to +3% (grocery), and varied among days with average within-day mobility changes (on the same day but across all districts) ranging from +1% to +32% (homes), −51% to + 143% (parks) and −65% to +27% (grocery).

(b) Effect of human mobility on bird counts

Most of our focal species (20/25; 80%) were significantly affected by human mobility changes during the pandemic. Of these affected species, most (16/20) altered habitat use in response to several measures of human mobility. Counts of over half of affected species (11/20 species) changed when humans changed the amount of time they spent at home, parks (13/20 species) and grocery locations (12/20 species) (table 1; see electronic supplementary material, table S6 for detailed model results).

Time spent at home affected the counts of approximately one-quarter of focal species, with counts slightly more likely to be lower (4/7 species) when humans spent more daily time at home, and over the long-term seasonal time frame in districts where humans spent more time at home throughout the lockdown (4/6 species). Human time spent at parks affected the greatest number of species (10 and 7 species, for short-term daily and long-term seasonal mobility changes, respectively), with counts of some species increasing and others decreasing as time in parks increased. Effects of short-term daily park use were the reverse of long-term seasonal effects; counts of 70% (7/10) of species were higher on days when humans spent more time at parks, while counts of 71% (5/7) of species were lower over the long term when humans spent more time at parks. Counts of approximately one-third of species (eight and seven species, for short-term daily and long-term seasonal mobility changes, respectively) were correlated with visits to grocery locations; all affected focal species had lower counts on days when humans increased visits to grocery locations, over both the short-term and long-term time scales (table 1).

(c) Short-term daily effects

Short-term effects of reduced daily human mobility resulted in almost equal numbers of species increasing or decreasing in counts when humans stayed at home more (table 1, figure 2). As time at home increased, more blackbirds, dunnocks and woodpigeons were counted, whereas fewer great tits, wrens, rooks and buzzards were counted (table 1).

Most species had higher counts on days when humans spent more time at parks (table 1, figure 2). Rooks, jackdaws, mallards, lesser black-backed gulls, black-headed gulls, herring gulls and buzzards all had higher counts when humans used parks more, although great tits, blue tits and house sparrows showed the opposite pattern. Blackbirds, song thrushes, wrens, chaffinches, rooks, black-headed gulls, buzzards and collared-doves all had higher counts when humans visited grocery stores less frequently during the pandemic (table 1, figure 2).

(d) Long-term seasonal effects

Approximately half of our focal species (14/25 species) were affected by long-term changes in human mobility (table 1). Counts of blackbirds, jackdaws, magpies and wood pigeons were lower, while goldfinches and lesser black-backed gulls counts were higher in districts where humans spent more time at home over the duration of the lockdown (table 1). Surprisingly, although increased visits to parks tended to result in greater bird counts on a daily basis, the reverse was true when considering long-term mobility effects, such that more human activity in parks over the duration of the lockdown resulted in decreased detections of birds. This pattern was generally driven by gulls and corvids. Carrion crows, rooks, mallards, black-headed gulls and herring gulls were all observed in fewer numbers while counts of dunnocks and collared-doves were observed more in districts where human visited parks more over the duration of the lockdown. Blackbirds, dunnocks, chaffinches, goldfinches, jackdaws, magpies and black-headed gulls all had higher counts in districts where human went to the grocery locations less over the duration of the lockdown (table 1).

Six species showed different patterns at daily versus long-term seasonal effect scales. Counts of blackbirds and wood pigeons were higher on days when humans spent more time at home (figure 3*a*,*c*, table 1); however, counts were lower over the long term when humans spent more time at home over the duration of the lockdown (figure 3*b*,*d*, table 1). Similarly, rooks, mallards, black-headed gulls and herring gulls had greater counts when humans visited parks more (figure 3*e*,*g*, table 1), but fewer counts over the long term when humans used parks more on average during the lockdown (figure 3*f*,*h*, table 1).

(e) Taxonomic patterns

Impacts of human mobility varied within and among taxonomic families (table 1). Feeder birds (electronic supplementary material, table S3), which varied in body mass [57], varied in their response to human mobility at home and at parks. Tits (blue tit and great tits), which are small-bodied garden feeder species [57], had lower counts when humans spent more daily time at home or at parks. Finches (chaffinch, goldfinch and greenfinch), which are also small garden feeders, were not affected by short-term changes in human mobility at home and at parks. Most of our focal species that exploit human refuse and roadkill such as corvids, gulls and buzzards increased in counts when humans spent more daily time at parks. However, over the long term, rook, black-headed gull and herring gull counts decreased when humans spent more time at parks (table 1).

(f) Detectability

Data on changes in detectability near roads [56] was available for 22/25 of our focal species; data were unavailable for all three of our gull species (*Chroicocephalus ridibundus*, *Larus argentatus* and

Table 1. Effects of human mobility on bird counts during the pandemic, in comparison with the pre-pandemic period. Home = 'increase' means that bird counts increased as human spent more time at home, while home = 'decrease' means that bird counts decreased as human spent more time at home. Humans spent more time at home during the pandemic (figure 1), so species that increased counts were detected more often during the pandemic than in the previous years, and species that decreased counts were detected less often during the pandemic. Parks = 'increase' means that bird counts increased as human spent more time at parks, while park = 'decrease' means that bird counts decreased as human spent more time at parks. Time spent at parks generally increased during the pandemic, so species that increased counts were detected more often during the pandemic than in the previous years, while species that decreased counts were detected less often during the pandemic. Grocery = 'increase' means that bird counts increased as human spent more time at grocery locations, while grocery = 'decrease' means that bird counts decreased as human spent more time at grocery locations. Humans spent less time at grocery locations during the pandemic (figure 1), so species that decreased counts were detected more often during the pandemic than in the previous years.

			short-term daily effects			long-term seasonal effects		
species	Latin name	family	home	parks	grocery	home	parks	grocery
Eurasian blackbird	*Turdus merula*	Turdidae	increase		decrease	decrease		decrease
song thrush	*Turdus philomelos*	Turdidae			decrease			
Eurasian blue tit	*Cyanistes caeruleus*	Paridae		decrease				
great tit	*Parus major*	Paridae	decrease	decrease				
long-tailed tit	*Aegithalos caudatus*	Paridae						
European robin	*Erithacus rubecula*	Muscicapidae						
Eurasian wren	*Troglodytes troglodytes*	Troglodytidae	decrease		decrease			
dunnock	*Prunella modularis*	Prunellidae	increase				increase	decrease
house sparrow	*Passer domesticus*	Passeridae		decrease				
common chiffchaff	*Phylloscopus collybita*	Phylloscopidae						
common chaffinch	*Fringilla coelebs*	Fringilidae			decrease			decrease
European goldfinch	*Carduelis carduelis*	Fringilidae				increase		decrease
European greenfinch	*Chloris chloris*	Fringilidae						
carrion crow	*Corvus corone*	Corvidae					decrease	
rook	*Corvus frugilegus*	Corvidae	decrease	increase	decrease		decrease	
Eurasian jackdaw	*Corvus monedula*	Corvidae		increase		decrease		decrease
Eurasian magpie	*Pica pica*	Corvidae				decrease		decrease
mallard	*Anas platyrhynchos*	Anatidae		increase			decrease	
lesser black-backed gull	*Larus fuscus*	Laridae		increase		increase		
black-headed gull	*Chroicocephalus ridibundus*	Laridae		increase	decrease		decrease	decrease
herring gull	*Larus argentatus*	Laridae		increase			decrease	
common buzzard	*Buteo buteo*	Accipitridae	decrease	increase	decrease			
rock pigeon	*Columba livia*	Columbidae						
Eurasian collared-dove	*Streptopelia decaocto*	Columbidae			decrease		increase	
common wood pigeon	*Columba palumbus*	Columbidae	increase			decrease		

Larus fuscus). Of the 18 species that were less detectable near roads [56], only four species increased in counts during the pandemic (electronic supplementary material, table S7). Of three species that were more detectable near roads [56], none decreased in counts during the pandemic (electronic supplementary material, table S7). This suggests that most changes in bird counts associated with human mobility changes were unlikely to have resulted from traffic-associated changes in bird detectability.

4. Discussion

Human mobility changes during the pandemic resulted in changes in counts of most of our focal species (20/25 species), as predicted, and consistent with other studies that have also demonstrated that wildlife altered habitat use [17,18,24,25,27,29,30] or changed behaviours [28] during the pandemic lockdowns. Behavioural responses to mobility changes varied with species, human mobility type (home, parks and grocery), and time scale (daily short-term and long-term seasonal). Contrary to our predictions, smaller bodied species were not more likely to respond to human mobility changes compared to larger species. We also found mixed support for changes in bird counts that could be attributed to changes in the focal species food resource; for example, we did not find evidence that feeder species were detected more during the pandemic; however, some species that eat carrion and human food refuse increased counts during the pandemic, suggesting that for these species, changes in human-sourced foods may have affected habitat use. Taxonomically related species often had similar responses to changes in human mobility, although there was also variation in the degree of response to human

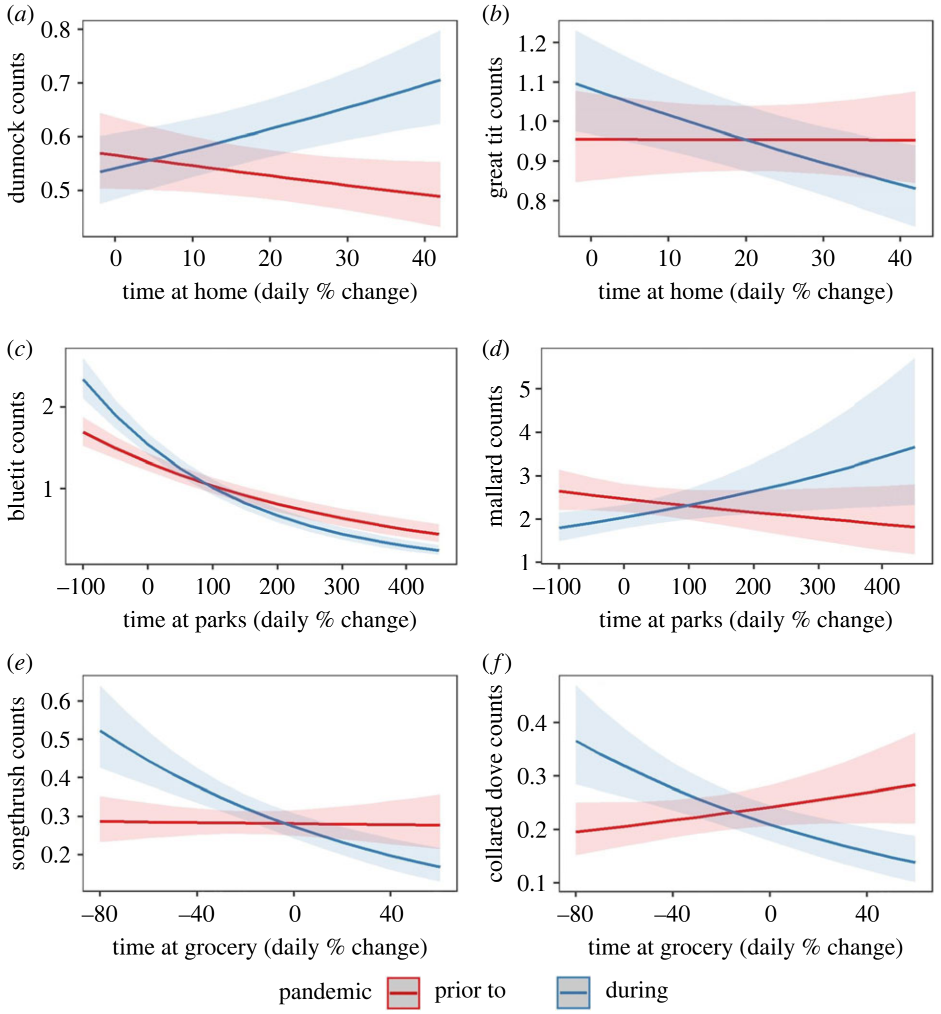

Figure 2. Examples of significant daily effects of changes in human mobility on predicted bird counts measured from 1 March to 4 July 2017–2020. For conciseness, we show examples of effects here; for complete results, see electronic supplementary material, S4. Here, (*a*) shows an increase in bird counts when humans spent more time at home, while (*b*) shows a decrease when humans spent more time home. For parks and grocery, (*c*,*e*,*f*) show a decrease in counts when humans spent more time at those locations while (*d*) shows an increase. No decreased counts were observed in any of our focal species in response to changes in grocery mobility. (Online version in colour.)

mobility within families. Clearly, there are complex relationships between the lockdown, the change in human behaviours that ensued, and wildlife communities, and this resulted in a wide range of behavioural responses among species and regions.

As human-dominated environments and activities create multiple selection pressures that operate simultaneously [58], different types of human mobility (home, parks and grocery) may result in different selection pressures that in turn affect avian habitat selection and use. Roads and vehicular traffic can be selective pressures that alter the survival, fitness and behaviours of wildlife [59]. During the pandemic, decreases in vehicular traffic resulted in less noise [28,29], air pollution [60] and traffic mortality [19–21,29], which increased habitat use by some bird species within many kilometers of roads [30]. Thus, bird count increases in response to decreased vehicular traffic suggest that traffic levels might have been suppressing avian abundances prior to the pandemic, as seen in North America and Italy [29,30]. One of our most striking results is that in the UK, all 12 affected species (table 1) had increased counts on days and in districts when humans visited grocery locations less. The most likely explanation for this is that fewer trips to grocery stores resulted in less vehicular traffic and associated disturbances, which consistently benefited birds and made them more available for counts during eBird surveys. By contrast, time spent at home and in parks were associated with a variety of altered human behaviours that had differing impacts (e.g. increased or decreased traffic, disturbance from humans and pets outdoors, impacts on local vegetation and food provisioning; see also [58]) on the number of birds detected. This may explain the substantial variation in species responses to changes in the amount of time humans spent at home and in parks.

In the UK, residential gardens comprise one-quarter of urban land cover [61] and are an important habitat type for British birds [11]. Resource provisioning has contributed to national-scale population changes, with common feeder species, such as goldfinches and wood pigeons, increasing in abundance at higher rates than species that avoid garden habitats [11,42]. We predicted that feeder birds might benefit from more consistent replenishment of feeders during lockdowns, as well as by decreased traffic associated with increased time at home. However, the opposite was true, as observations of several feeder species (daily short term: great tits, Eurasian wrens; long-term seasonal: blackbird, wood pigeon) were less frequent when time spent at home increased. We speculate that disturbance from people and pets spending more time in home gardens resulted in the displacement of feeder birds from sites they normally use. While foraging opportunities likely explain some of the patterns in behavioural changes we observed during the pandemic, human disturbance likely interacted with food availability [42], resulting in complex impacts of lockdowns on birds of the UK.

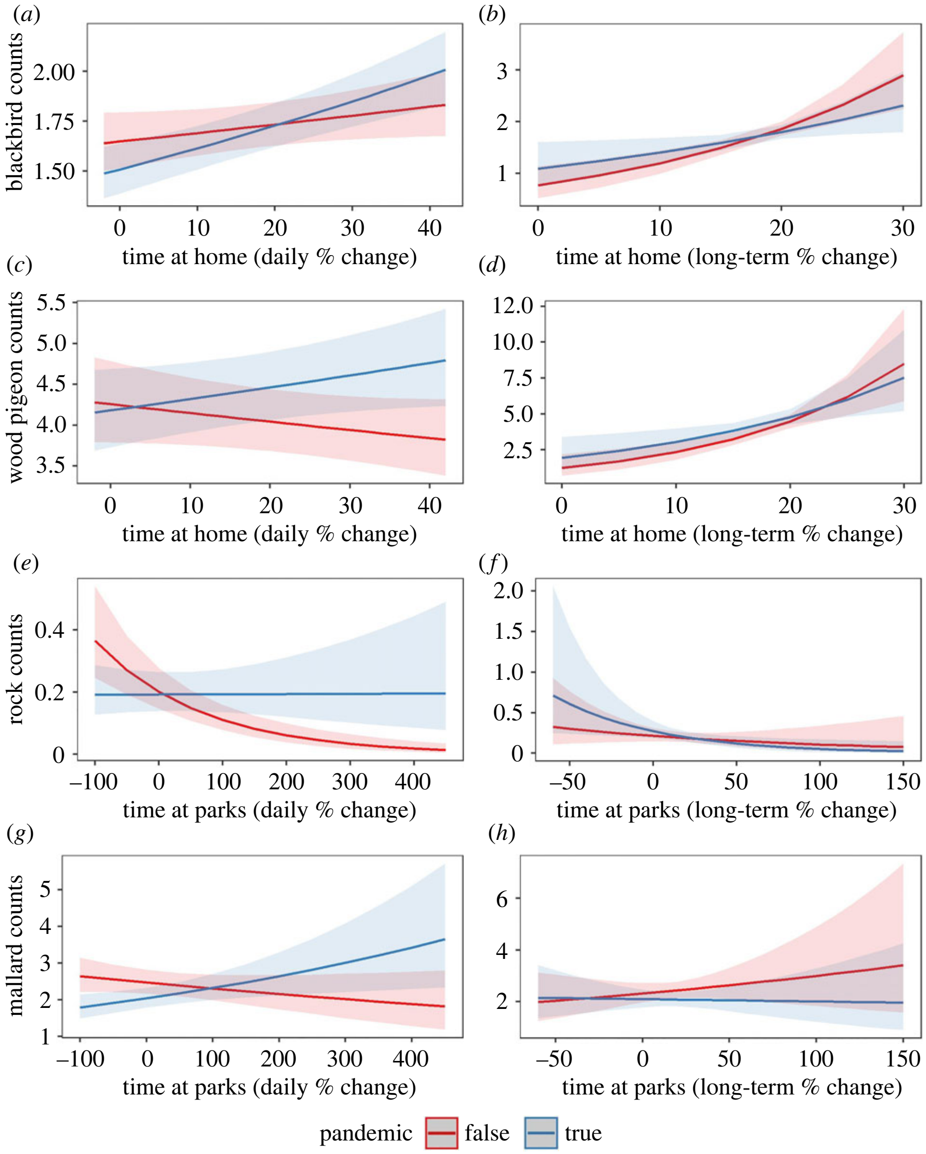

Figure 3. Examples of differences in species response to daily effects (daily % change) versus long-term seasonal effects (average % change) in human mobility on predicted bird counts measured from 1 March to 4 July 2017–2020. For conciseness, we show examples of effects, rather than all significant results (see electronic supplementary material, table S4). The left-hand column (*a,c,e,g*) show examples of daily mobility effects, and the right-hand column (*b,d,f,h*) show long-term seasonal effects. Black-headed gulls and herring gulls had similar results to that of rooks. (Online version in colour.)

Similarly, parks and recreational green spaces provide bird habitat, and may also be associated with human-sourced food and disturbances [62]. We predicted that birds that benefit from human-sourced food that may be available in parks (e.g. picnicking refuse and recreational duck feeding), would have increased detections when humans spent more time at parks. Indeed, mallards and gulls (lesser black-backed gull, black-headed gull and herring gull) counts increased when humans spent more time in parks (daily time scale); however, most of these species had lower counts in districts with more visits to parks, perhaps because prolonged human activity, vehicular traffic and disturbance have negative impacts even on species that benefit in some ways from humans [39]. Contrastingly, smaller species that forage on natural food resources available in parks (e.g. Eurasian blue tits, great tits and house sparrows) had lower counts when humans spent more daily time at parks, demonstrating again that human disturbance may have had negative impacts on some species of birds.

Roadkill is an important food resource for some scavenging bird species [63]. We also predicted that birds that might have previously benefited from carrion food resources resulting from vehicular activity (i.e. roadkill) may have been impacted by a decrease in roadkill carrion as humans drove less during the pandemic [19–23]. Counts of some carrion-eating species decreased when humans stayed at home more (daily short term: rook, buzzard; long-term seasonal: jackdaws and magpies), or increased when human visited parks more (daily short term; rook, jackdaw and buzzard). Contrastingly, over the long term, counts of some carrion-eating species (e.g. carrion crow and rook) decreased in districts where humans visited parks more, which could be related to long-term disturbance in park habitats.

Our findings are consistent with other studies that have suggested that changes in foraging behaviours of animals during the pandemic were associated with changes in the availability of human-sourced food [17,18]. For example, in Australia, Torresian crows (*Corvus orru*) moved from urban areas where they scavenge for human-sourced foods, to beach areas during the pandemic [17]. In Singapore, Javan mynas (*Acridotheres javanicus*) decreased abundance in green spaces, while increased in numbers at refuse collection centres, while feral pigeons (*Columba livia*) decreased abundance in urban food centres [18].

An animal's tolerance to human presence or resources may vary with body size [41]. Thus, when humans increased time at home or parks, changes in human disturbance and resource availability (feeder provisioning) may have altered habitat suitability for different species relative to their body size. We predicted that smaller bodied species will have been more likely to change bird counts in response to human mobility changes, compared to larger species. Surprisingly, however, smaller bodied species (less than 50 g; Eurasian blue tit, great tit, long-tailed tit, European robin, Eurasian wren, dunnock, house sparrow, common chiffchaff, common chaffinch, European goldfinch, European greenfinch; for mass ranges see electronic supplementary material, table S3) did not respond more to changes in human mobility than medium or large sized birds. For example, only great tits, European wrens, dunnocks and goldfinches had different bird counts during the pandemic lockdowns when humans stayed at home (short term and long term), compared to pre-pandemic years. Contrastingly, larger birds (blackbirds, rooks, buzzards, wood pigeons, jackdaws, magpies, lesser black-backed gulls and wood pigeons) had different counts during the pandemic compared to pre-pandemic years when humans stayed at home (short term and long term). However, tolerance to human disturbance may be associated with other species traits such as habitat and diet breadth [12], boldness and explorative tendencies [58], and behavioural flexibility [4]. As human presence in gardens has already led to changes in the UK avian community by favouring generalist, and dominant aggressive species [11,42,57], many garden species may already have been adapted to human presence in gardens prior to the pandemic, perhaps explaining why some garden species, such as long-tailed tits and European robins, were observed in equal numbers before and during the pandemic.

Species responses to human disturbance may be associated with evolutionary history, such that closely related species may have similar responses to disturbance (e.g. [39]). We found that multiple species from the same taxonomic family (e.g. Paridae, Corvidae and Laridae) tended to have similar responses to human mobility changes. Interestingly, responses of some taxonomic groups were similar between UK and North American populations [30]. For example, in both the UK and North America, some tits (Paridae) and corvids (Corvidae) had lower counts in districts where humans stayed at home over the lockdown period (this study, and [30]). Mallard (*Anas platyrhynchos*) counts decreased in North American urban areas [30] and with increased long-term seasonal human mobility at parks in the UK, perhaps suggesting an association between mallards and human-sourced food (i.e. duck feeding).

Many invasive species have evolved adaptations to their novel environments [4]. For example, house sparrows are native in the UK where they have suffered population declines [64], while North America populations are invasive and differ behaviourally and genetically from UK populations [65]. House sparrows showed no behavioural responses to lockdown in North America [30], but decreased in counts when humans increased daily park use in the UK, suggesting sensitivity to human disturbance. Thus, high levels of human activity disturbance may affect UK populations of house sparrow, whereas invasive sparrow populations in North America may be more tolerant of human activity.

(a) Study limitations

We note that the changes in birds detected during lockdowns relative to observations submitted by eBird participants in previous years may have resulted either from birds changing their locations during the pandemic (leaving or entering the areas surveyed), or changing their behaviour locally (e.g. moving out of visible range of detection and thus becoming more cryptic, e.g. hiding within or below vegetation canopies). In either case, we argue this represents a behavioural response of birds to lockdowns by altering their habitat use at a range of small to moderate spatial scales and are unlikely to reflect changes in population sizes during the relatively short period of the first COVID-19 lockdowns. We ensured that equal numbers of checklists were surveyed during and before lockdowns at the scale of 3 km cells, but we note some birders may have changed their survey behaviour during lockdowns at an even smaller spatial scale within cells. eBird data showing locations of survey routes are not publicly available, so we could not test whether this was the case, and interpretation of our results should bear this in mind.

Google Mobility data showed significant changes in human mobility at home, parks and grocery locations, and our findings indicate that these different mobility types have differing effects on bird counts. However, even though humans spent more time at home during lockdowns, humans may have varied in how they spent their home time [66], with some humans spending more time in gardens than others. On average, increases in human mobility probably led to humans spending more time in gardens, as greater than 78% of Britons have access to gardens [66] and spent more time gardening during lockdowns [66]. However, as Google Mobility data cannot differentiate between humans spending more time in their gardens, versus time indoors their residences, further studies are needed to disentangle the effects of multiple human behaviours at home on wildlife responses.

Additionally, although we examined effects of changes in detectability on bird counts from the perspective of road-associated disturbances, other changes in human activity could influence the bird behaviours that alter detectability [56]. For example, human presence may have altered the 'landscape of fear' in parks and therefore may have caused birds to decrease activity in response to an increased perception of predator risk [67], thereby lowered bird detectability to human observers. Thus, further studies examining the species- or habitat-specific responses to changes in human mobility and behaviours are necessarily to fully understand the impacts of human mobility changes during the pandemic.

Future studies are also needed to understand the eco-evolutionary impact of avian behavioural changes during the pandemic lockdowns. For example, increases or decreases in the use of certain habitats by birds do not necessarily translate to benefits/costs to their populations or reproductive success (e.g. [38,39]. Nonetheless, it is clear that the impacts of pandemic lockdowns on birds varied significantly and in highly ecologically important ways.

5. Conclusion

Birds interact with human communities in complex ways, and during the worldwide upheavals associated with COVID-19, human activity drastically changed. In the UK, this has affected the habitat use of many species, potentially leading to unknown population-scale or generational eco-evolutionary impacts on wildlife. Although many environmentalists intuitively assumed that decreased human activity would ultimately benefit wildlife, our results showed that not all bird species responded in the same way, and response to human activity was influenced by human activity type and the time scale of the disturbance. Examining how different species responded to these sudden and drastic environmental changes during the pandemic lockdown gave support for the hypothesis that response to HIREC is influenced by species traits that may be linked to evolutionary adaptations such as body size and food resource use, although further studies are needed to explore these associations. Furthermore, short-term benefits of human-sourced supplemental food may have been outweighed by long-term disturbance. Ultimately, dramatic changes in human activity during pandemic lockdowns resulted in significant impacts across avian communities, demonstrating that humans have complex and important impacts on wildlife, even when we are 'staying home'.

Data accessibility. Data and code can be accessed from the Dryad Digital Repository: https://doi.org/10.5061/dryad.15dv41p14 [68].

The data are provided in the electronic supplementary material [69].

Authors' contributions. M.H.W.: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing—original draft and writing—review and editing; M.B.S.: conceptualization, data curation, formal analysis, methodology and writing—review and editing; P.D.B.: conceptualization, methodology and writing—review and editing; M.E.T.: conceptualization, data curation and writing—review and editing; N.K.: conceptualization, funding acquisition, methodology, supervision, validation, writing—original draft and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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