Species and habitat specific changes in bird activity in an urban environment during Covid 19 lockdown

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Abstract

Covid-19 lockdowns provided ecologists with a rare opportunity to examine how animals behave when humans are absent. Indeed many, sometimes contradicting, studies reported various effects of lockdowns on animal activity, especially in urban areas and other human-dominated habitats. We explored how Covid-19 lockdowns in Israel have influenced bird activity in an urban environment by using continuous acoustic recordings to monitor three common bird species that differ in their level of adaptation to the urban ecosystem: (1) the hooded crow, an urban exploiter, which depends heavily on anthropogenic resources; (2) the rose-ringed parakeet, an invasive alien species that has adapted to exploit human resources; and (3) the graceful prinia, an urban adapter, which is relatively shy of humans can be found urban habitats with shrubs and prairies. Acoustic recordings provided continuous monitoring of bird activity without an effect of the observer on the animal. We performed dense sampling of a 1.3 square km area in northern Tel-Aviv by placing 17 recorders for more than a month in different micro-habitats within this region including roads, residential areas and urban parks. We monitored both lockdown and no-lockdown periods. We portray a complex dynamic system where the activity of specific bird species decreases or increases in a habitat-dependent manner during lockdown. Specifically, urban exploiter species decreased their activity in most urban habitats during lockdown, while human adapter species increased their activity during lockdown especially in parks where humans were absent. Our results also demonstrate the value of different habitats within urban environments for animal activity, specifically highlighting the importance of urban parks. These species- and habitat-specific changes in activity might explain the contradicting results reported by others who have not performed a habitat specific analysis.

Introduction

Covid 19 lockdowns provided a unique opportunity to examine the effects of humans on wildlife presence and activity (Rutz et al., 2020). The public media was full of reports on animals that have supposedly taken over areas that are most of the time occupied by human activity. Several studies reported animals expanding their behavior to day-time (Manenti et al., 2020), or venturing deeper into urban areas during the COVID-19 lock-downs (Vardi et al., 2021). Several studies reported an increase in avian abundances in urban habitats (Schrimpf et al., 2021). More careful quantifications however, casted doubts on these reports (Vardi et al., 2021; Gordo et al., 2021). These discrepancies in the responses of species to the lockdowns could have stem from the fact that species may differ in their levels of adaptation to human activity (Lowry et al., 2013). Furthermore, most studies focused on specific urban habitats such as large green spaces which represent only a small fraction of the diverse urban landscape (Shwartz et al., 2014). There is therefore a need to explore how species with different levels of adaptation to human activity were affect by the lockdowns across habitats to advance the understanding of the effect of humans on wildlife presence and activity. Moreover, most previous studies have relied on human (citizen) sporadic reports, which can be biased as they were also dependent on changes in human activity (Vardi et al., 2021), or on observer-based surveys, which may affect bird activity (Browning et al., 2017). Using passive acoustic recordings, as we did, holds an interesting opportunity to tackle some of these issues and allow for more objective disturbance free monitoring of wildlife activity (Browning et al., 2017).

Acoustic monitoring has been on the rise as a useful method for assessing insect (Penone et al., 2013), bat (López-Bosch et al., 2022) and bird (Pérez-Granados et al., 2021) diversity. This methodology has several clear advantages: it is continuous, and does not require the observer to be present and thus the animals are not affected by the measurement itself (Shonfield & Bayne 2017; Gibb et al., 2019). Acoustic recordings are cost-effective, especially with the development of modern cheap recorders, and they are efficient in dense environments where the animals cannot be easily detected such as dense forests or urban environments. Additional advantage is that the data collected using acoustic recordings can be reanalyzed and reinterpreted as new questions arise, or when looking for new species (Borker et al., 2014; Pérez-Granados & Schuchmann 2020). These recordings can also be used to monitor human activity which allows to evaluate the impact of local human disturbance (Buxton et al., 2018). Finally, they allow estimating ambient noise levels (Alfaro-Rojas et al., 2020), as well as changes in the acoustics of the vocalizations which can indicate adaptations of animal communication (de Framond et al., 2022). Thus, acoustic recordings provide an excellent opportunity to monitor various species across urban habitat in a standardize manner.

In this study we aimed to examine the effects of the reduced human activity during the Covid 19 lockdown on species that represent different levels of adaption to humans and exploitation of the urban resources across different types of urban habitats in Tel-Aviv Israel. Research exploring biodiversity response to urbanization has classified species into three main groups regarding their level of adaptation to human activity and their ability to exploit anthropogenic resources (Blair 1996; Kark et al. 2007): (1) urban avoiders, species that are particularly sensitive to human induced changes and reach their highest densities in natural environment outside the urban area; (2) urban adapters, species that thrive in urban green spaces, as they have adapted to exploit green urban resources (e.g., ornamental vegetation); and (3) urban exploiters, species that adapted to exploit the resources provided by humans in the urban environment and therefore reach high densities in the most built environments. These species together with non-native invasive alien species that have also adapted to exploit various human green and grey resources often replace a wider range of native species in a process that was describe as the biotic homogenization (Lockwood & McKinney 2002; Crooks et al., 2004).

Building on previous studies that were conducted in Israel and classified common bird species to the three groups (Kark et al., 2007; Colleony & Shwartz 2020), we selected three widespread and common urban species that vary in their level of adaptation to human activity. The hooded crow (*Corvus corone cornix*) is a native urban exploiter that heavily depends on anthropogenic resources for foraging and breeding and can be found in all types of urban habitats (Kark et al., 2007). The rose-ringed parakeet (*Psittacula krameri*) is a non-native urban adaptor that thrives in Israel and elsewhere due to its ability to adapt and exploit different types of human resources (e.g., ornamental plants for feeding and infrastructure of breeding; White et al., 2019). The Graceful prinia (*Prinia gracilis*) is an insectivorous species that is relatively shy of humans and can be found in various green spaces where there are shrubs and prairies that represent it main habitat. The first two species can be considered as urban exploiters or synanthropic species that currently thrive and their population is increasing in Israel, while the one represent an urban adaptor with population that currently decreasing in Tel-Aviv and across the country (Colléony & Shwartz 2020).

We performed our study around the first lockdown period in Israel (March-May 2020). The exact bird detection range of our method is hard to estimate accurately (because it depends on many parameters such as the building coverage) but we estimate it to be ~50 m. In light of the complex mosaic of urban habitats, we compared activity in three micro-habitats within cities, namely, in parks, roads and residential areas. We performed our monitoring at 17 sites in central Tel-Aviv on average ~200 m apart from each other. The region we monitored included residential areas with small parks scattered within them and with small-medium sized roads connecting them. Buildings in this region are usually surrounded by small gardens, which will typically have some fruit and other trees. The north-most sector of the region includes a large open habitat on the bank of the Yarkon river (Yarkon Park), recognized as the main bird source in Tel-Aviv and servicing as green corridor connecting the city to more natural environments around it (Figure 1A; Shwartz et al., 2008).

We examined various models and found changes in bird activity that are species and habitat specific. We find that human following species moved their activity to residential areas during lockdown, in contrast to a human aversive species that increased its activity in all habitats in the absence of humans. Our results thus demonstrate the importance of micro-habitats within the urban environment and highlight the complexity of nature's response to a dramatic shift in human activity.

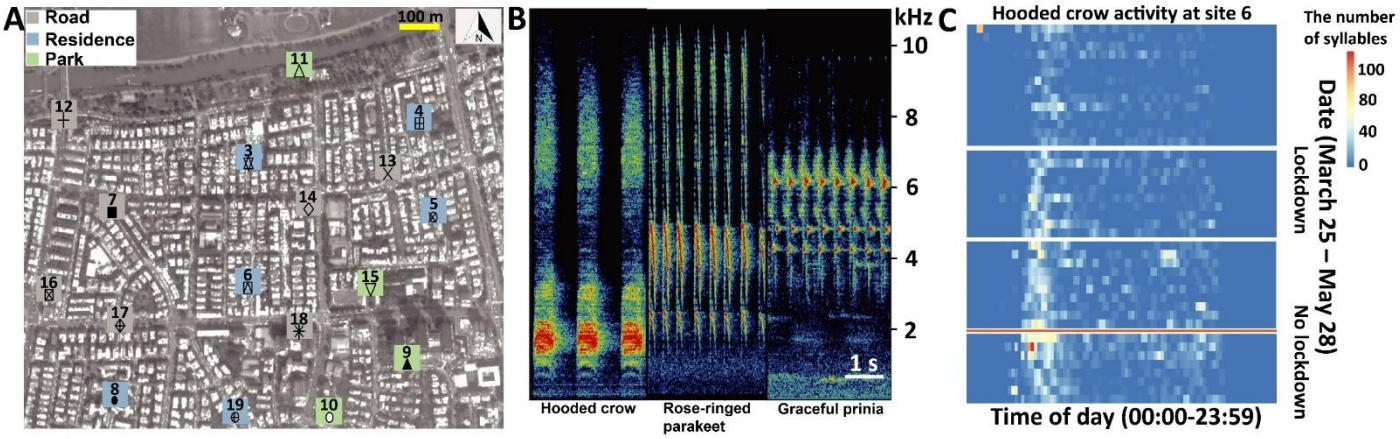

Figure 1. Study system, vocal characters and vocal activities. (A) The seventeen sampling sites (Grey square: road; Blue square: residence; Green square: Park). The total activity for each species at each location is shown in bars for the lockdown (red) and no-lockdown (blue) periods. Different sampling sites are represented by different symbols. (B) Spectrograms of vocalizations with Hooded crow, Rose-ringed parakeet, and Graceful prinia. (C) An example of a heat-

map indicating the activity of Hooded crow at site 11 monitored continuously between March 31 – May 28 (without the dates between April 9 – April 23, May 4 – May 6, May 17 – May 20, depicted by white gaps). The x-axis depicts the time of day (not normalized to sunrise). The y-axis is the date. The red horizontal line separates lockdown from no lockdown periods. The figure also suggests an overall seasonal increase in activity, but our models suggest a lockdown effect on top of this seasonal effect.

Results

We analyzed 388,080 audio recordings accounting for a total duration of 3,234 hours from 17 sites (Figure 1A). In total we detected 52,080 files with 72,824 syllables of Hooded crows, 33,654 files with 73,445 syllables of Rose-ringed parakeets and 21,800 files with 117,982 syllables of Graceful prinias. The distribution of the audio recordings along the sampling periods can be found in Table S3-S5 in Supplementary material 1. A detailed summary of the activity of each species at each site can be found in Supplementary materials 2-3-4 (and in Figure 1A). We used these vocalizations to assess birds' spatio-temporal activity. We referred to the total number of events (i.e., files) detected per species as its total daily activity. We also estimated daily activity variability by calculating the coefficient of variance of number of daily events. Dynamic illustrations of the changes in bird activity are presented in Supplementary movies 1-3. As expected, human activity significantly increased in residential areas by 49% during the lockdown and significantly decreased in parks by 31% as visiting parks was forbidden (Figure 2A; Table S6 in Supplementary material 5).

Bird activity

When analyzing the activity of all species together, we found that the bird species and site type (park, road, residential) had a significant effect on activity, and moreover, that the interaction between the lockdown status and the species was also significant (Table 1). Below, we thus analyze the effect of the lockdown status on each species of bird separately. However, a few general patterns were observed from the analysis of all species together. Bird activity (number of daily events) was overall always highest in parks (62% more than near roads and 53% more than in residential areas, Table 1). Bird activity significantly decreased with an increase in ambient noise levels (Table 1). The average effect size was a reduction of 6% in activity per 1 dB of noise. As expected, ambient noise levels during the lockdown were significantly lower by an average of ca. 1.5 dB for crows, 1.7 dB for parakeets, and 1.7 dB for Prinia (LMM: $-1.5 < \text{estimate} < -1.3$, $-7.5 < t < -5.2$, $P < 0.0001$; the noise was estimated for each species in its call's peak frequency, Figure S1 in Supplementary material 5), but this reduction in noise was no enough to explain changes bird activity the lockdown (Table 1). The overall bird activity also significantly increased with an increase in temperature (by 5% per degree, Table 1).

We also examined the variability of the activity for all species together. Note that a reduction in the coefficient of variance per day means that activity is more constant, or less variable during the day. Overall, the coefficient of variance showed opposite patterns in comparison with the activity, that is, whenever we observed more activity, we observed less variability and vice versa. When analyzing all species together, we found that the activity in roads and residential areas was significantly more variable than in parks (Table 1 and Table S7 in Supplementary material 5). Moreover, the variability significantly increased with an increase in noise, it increased during the lockdown periods, and it significantly decreased with an increase in temperature (Table 1 and Table S7 in Supplementary material 5). As with the total activity, the patterns were species and site specific, as analyzed and detailed below.

Given the differences between species and site type, we analyzed the effect of the above-mentioned parameters on activity and activity variability of each species. Hooded crow activity significantly decreased (by ~48%) during the

lockdown period (Figure 2B and Figure 1C), but the effect of the lockdown was not apparent at all site types (Table 1 for the full list of model parameters, and Table S7 in Supplementary material 5 for the model selection results). Post-hoc analysis revealed that while hooded crow activity decreased at all site types during the lockdown, these decrease was only significant in residential areas (by ~39%), and marginally significant in parks (Figure 2B; see Table S8 in Supplementary material 5 for full details). Hooded crows seemed to get used to the lockdown as activity increased along the lockdown period (GLMM: lockdown-countdown interaction, $P < 0.001$; Table 1). Note that our statistical models already take many of the lockdown ambient parameters into account including noise and human activity, so the significance we observe for the lockdown status might be due to additional lockdown related parameters (see discussion). In terms of their variability of activity, crows generally followed the opposite patterns with the variability behaving oppositely to the activity, and showing more variability with an increase in noise levels (Table 1 and Table S7 in Supplementary material 5).

Similar to Hooded crows, the activity of rose-ringed parakeets decreased during the lockdown in all site types, but this decrease was only significant in parks (by ~90%, see Figure 2C and Table S8 in Supplementary material 5). Parakeet activity also significantly increased with an increase in temperature (Table 1, Table S8 in Supplementary material 5). In terms of variability of activity, parakeets exhibited a significant decrease in variability during lockdown periods in residential areas and in parks, and no significant change near roads (Table S8 in Supplementary material 5). Parakeets exhibited more activity variability with an increase in ambient noise (Table 1, Table S7 in Supplementary material 5) and exhibited less variability with an increase in temperature (Table 1, Table S7 in Supplementary material 5).

Graceful prinias showed opposite patterns from both previous species exhibiting a significant increase in activity during the lockdown periods when examining all sites together (Table 1). When examining the site types separately, Prinia activity increased significantly during the lockdown in parks (by ~12%) and the increase in prinia activity in residential areas was marginally significantly (by ~7%), while there was no change near roads (Figure 2D; Table S8 in Supplementary material 5). Prinia activity decreased significantly with an increase in noise levels (Table 1) and significantly increased with an increase in temperature (Table 1). The increase during lockdown (vs. no lockdown) could not be explained as a result of seasonality because overall, prinia activity increased over time and the no-lockdown period was later in the season than the lockdown period. Prinia activity variability did not change significantly during lockdown periods (LMM: $P = 0.552$; Table 1). Prinia showed less variability with an increase in temperature (LMM: $P < 0.001$; Table 1). When examining each site type separately, activity variability did not change in residential sites and in roads but significantly decreased in parks (Table S8 in Supplementary material 5).

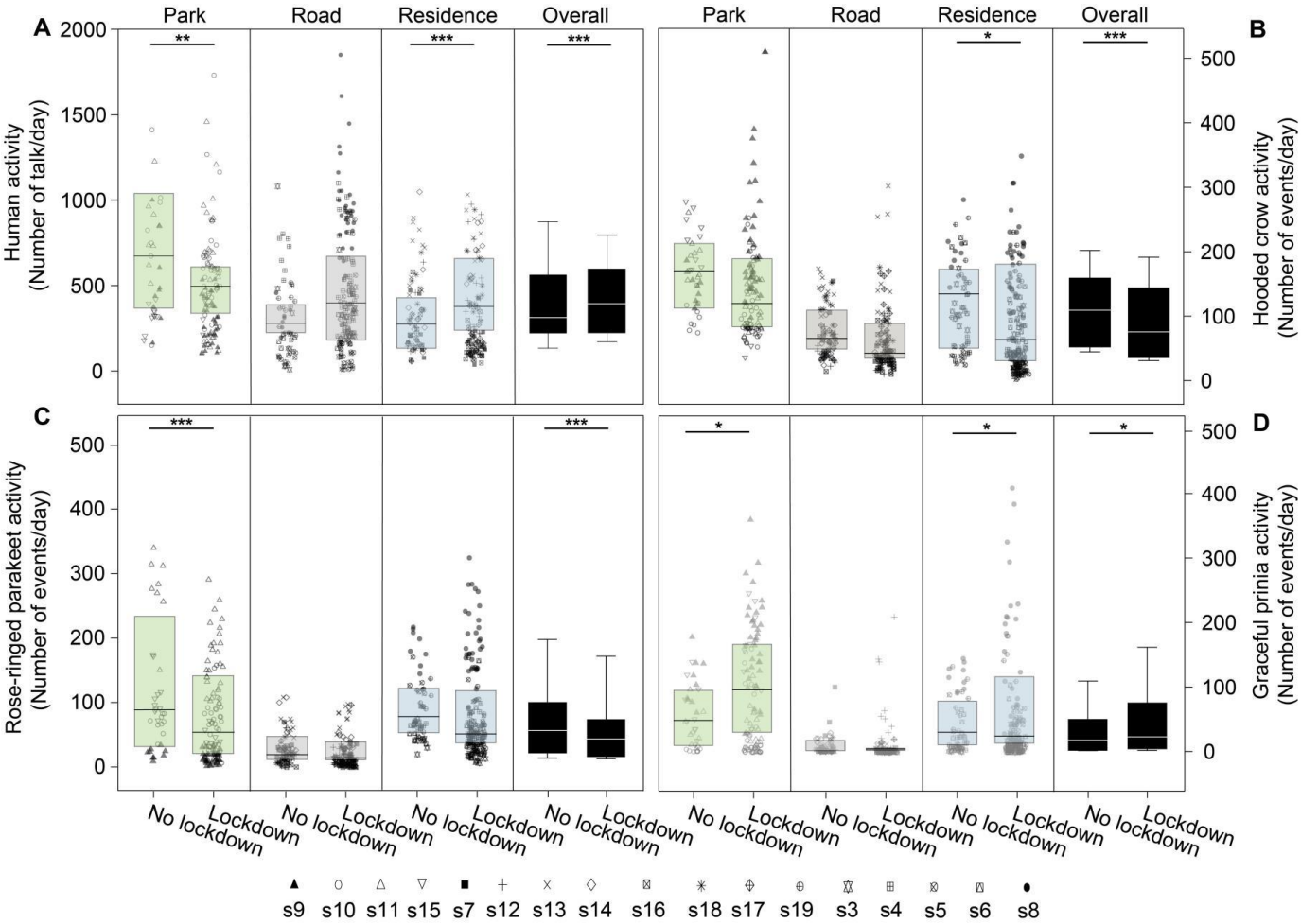

Figure 2. Activity of birds. Boxplots show the activity of (A) Human activity, (B) Hooded crow, (C) Rose-ringed parakeet, and (D) Graceful prinia for each site category during no lockdown and during lockdown. Green box plot: park; Grey box plot: road; Blue box plot: residence; Black box plot: overall. Note that human activity was assessed based on human speech so the increase observed during lockdowns in roads represents pedestrian and not car activity. Box plot lower and upper box boundaries show the 25th and 75th percentiles, respectively, with the median inside. The lower and upper error lines depict the 10th and 90th percentiles, respectively. Outliers of the data are shown as black dots. Different sampling sites represented by different symbols. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

We ran two models to control for the effect of our uneven sampling of the lockdown and no-lockdown periods: (1) We randomly selected five 10-day periods within the lockdown period and compared them to the no-lockdown period (where we also sample 10 days). This analysis revealed very similar results to the ones described above (for all five sub-samples) suggesting that our results were not an artifact of the imbalanced sampling (Figure S2-S6 in Supplementary material 5); (2) we performed a permutation test where we permuted the lockdown status of each day (while maintaining the number of lock-down and no-lock-down days constant). We performed 1,000 permutations and ran the GLMM model for each of the permuted data-sets (the GLMM was identical to the one presented in Table 1). We found that the estimate of the effect of lockdown was highest for the original data - higher than in all 1,000 permutations, suggesting that there was an additional effect of the lockdown on top of potential other effects such as the changes in noise and temperature.

Bird acoustics

In light of several studies that have reported changes in bird vocal acoustics during COVID-19 lockdowns, we also tested this for the three species we studied, examining call intensity and peak frequency (the most intense frequency)

for the recorded syllables (Table 2). All species seemed to produce louder vocalizations as ambient noise level increased. However, because they increased call intensity to a lesser degree than the additional noise, we conclude that this apparent increase was an artifact of the additional noise in the recordings rather than a real increase in source level. Specifically, we measured an increase of 0.35dB/noise dB for crows, 0.47dB/noise dB for parakeets, and 0.84dB/noise dB for prinias (Figure 3, LMM: all $P < 0.0001$ for all species; Table 2). We did not find any significant change in call frequency due to the lockdown (the vocalizations of rose-ringed parakeet had lower peak frequencies during lockdown, but the difference was negligible: ~4 Hz, Table 2).

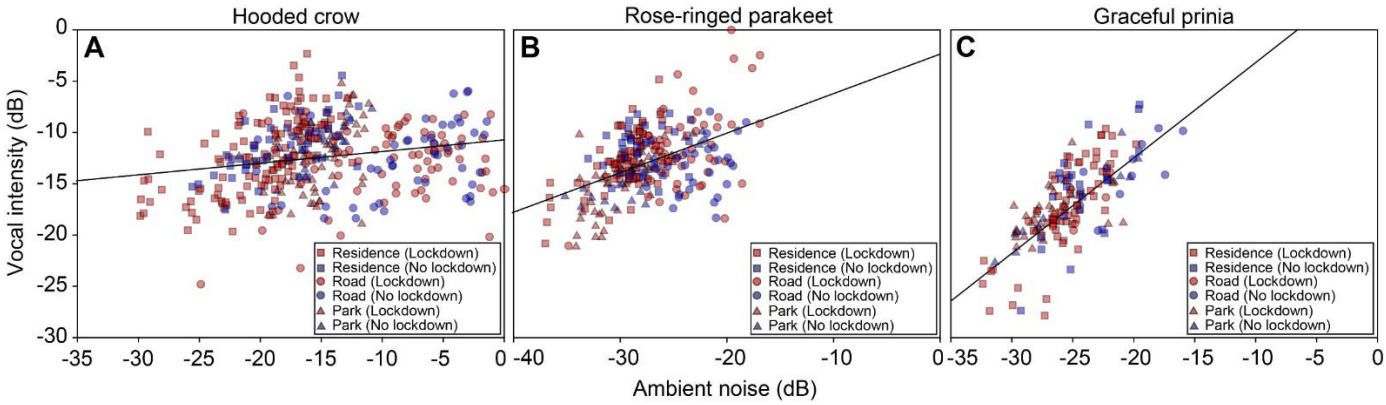

Figure 3. Vocal intensity as a function of ambient noise (normalized to maximum) for (A) Hooded crows. (B) Rose-ringed parakeets and (C) Graceful prinia. The lines depict the linear regression fit. Red colors and blue colors represent data collected during no lockdown and during lockdown, respectively (each point represents the average over one day). Square: Residences; Circle: Roads; Triangle: Parks.

Discussion

Animal activity during Covid-19 lockdowns has drawn much public attention with a popular notion that many species have reclaimed cities during lockdowns (Díaz & Møller 2023; Warrington et al., 2022; Behera et al., 2022). Monitoring citizen science reports of species demonstrated that these claims may have been exaggerated, and that species responded differently to the sudden and severe changes in human activity (Vardi et al., 2021). Yet, empirical evidence on how species activity vary during lockdown is scarce and knowledge is important to further understand how wildlife respond to human activity (Montgomrey et al., 2021). Our continuous acoustic monitoring of bird activity during lockdown and no-lockdown periods in an urban environment reveals a complex picture. On the one hand, synanthropic urban exploiter bird species such as the crows and parakeets, reduced their activity at all urban habitats. On the other hand, a non-synanthropic urban adapter song-bird, which typically sings from within vegetation, the Graceful Prinia, showed almost opposite patterns, increasing its singing activity during lockdown both in parks and in residential areas. Our main conclusion is thus that responses vary between species with different levels of adaptation to humans.

As expected, bird activity was correlated with several ambient factors such as temperature and noise (independently of the lockdown state). However, the changes in activity which we report for the lockdown period seem to be additional of changes in noise or temperature as these were accounted for in the models. Human presence (assessed by detecting human speech) could also not fully explain the shifts we observed in bird activity. Although the activity of all species significantly correlated with human presence but the presence of humans could not fully explain bird activity shifts. For instance, Crows and Parakeets decreased their activity in both parks and residential areas, even though human activity decreased in the former and increased in latter. It is likely that additional factors that were altered by the lockdown such

as other anthropogenic activities (e.g., cars) and the specific type of human activity (e.g., jogging and littering vs. walking) affected the birds' decision of activity. We also note that although we defined the lockdown as a binary state based on the official restrictions imposed by the government, in reality, humans gradually ignored parts of the restrictions in a non-binary manner.

We used bird vocalizations as a proxy for activity. This method has been validated by many other recent studies where bird vocal activity was found to be positively correlated with the abundance of birds (see a Review in Pérez-Granados & Traba 2021 and also Ducrettet et al., 2020; Pérez-Granados et al., 2021; Szymański et al., 2021). Using vocalizations to estimate activity is advantageous for many reasons as it allows collecting vast data over large spatio-temporal scales, but it also has its limitations. One challenge is distinguishing between changes in bird presence and changes in vocalizing. We made an attempt to rely on vocalizations that are used for intra-specific communication, but we could not assure that these vocalizations were not sometimes emitted towards predators such as humans. For parakeets, the great majority of vocalizations are used for communication between conspecifics and this is thus a good approximation for their presence and activity (Pruett-Jones et al., 2021). For crows, some of the vocalizations might be uttered during interactions with humans and thus, our results might be partially affected by the fact that there were less humans around during lockdown. Still, we argue that most crow vocalizations are directed towards conspecifics (Palestrini & Rolando 1996) and thus acoustic monitoring is a good way to assess their presence and activity. Moreover, crow activity decreased in both parks and residential areas even though human activity showed opposite patterns in these sites. The vocalizations of prinia were based on territorial male songs, so the increase we observed during lockdown, strongly suggests an increase in activity, even when accounting for the potential seasonal increase by adding temperature to the models. Bird activity is thus probably correlated with bird abundance, but we cannot determine for sure whether bird numbers changed during lockdown or whether the birds only changed their activity (i.e., interacted more and thus called more). Naturally, further studies are required to accurately connect changes in vocalization with changes in presence and activity. In addition to our analysis of the lockdown's effect, our results also clearly demonstrate the advantage of parks as safe havens for birds inside the urban environment – bird activity was always highest in parks regardless of lockdown condition (see Table 1). Interestingly, residential areas which in Israel are characterized by many trees also revealed much bird activity, in some sites - not significantly less than in parks.

Unlike some previous studies (e.g., Slabbekoorn & Peet 2003; Brumm 2004, Derryberry et al., 2020) we did not find any significant change in bird vocal acoustics during the lockdown periods. We note that such findings (reported by others) might be driven by signal processing artifacts resulting from changes in ambient noise and should thus be carefully examined. Finally, for some bird species, acoustic monitoring could also allow to distinguish between various behaviors, but we did not apply this approach here.

Various decisions have to be made when using acoustic monitoring, such as when do two adjacent recordings represent different individuals. We considered any recording of one of the three focal species within a file as one event thus ignoring the number of vocalizations within the file, however, we also tested a model which used the number of syllables (and not the number of files) as the explained variable, and this did not change the essence of the results (see Figure S7 and Table S9-S11 in Supplementary material 5). The distribution of the birds' syllables along the sampling periods can be found in Table S12-S14 in Supplementary material 6. Notably, when using visual surveying, this problem also exists because usually individuals cannot be distinguished and thus an individual bird appearing twice in the images (or binoculars) might be counted as two birds. Another potential concern is that changes in ambient noise might influence the detection rates and thus the results. Increased noise levels might make it difficult to detect weak vocalizations and

as a result imply a wrong reduction in activity. Because we used vocalizations that are far above the noise level of our recording system (see for example Figure 1B) the small changes observed in ambient noise could not explain our results. Moreover, we find both an increase and a decrease in activity (depending on site type and species) so our results cannot be explained by the unidirectional change in noise (i.e., the decrease in noise during lockdown).

Another potential bias in our experiment was seasonality - the lockdown stretched over almost two months during which spring shifted to summer and temperature increased by an average of two degrees. To control for this, we added temperature (which is a good proxy of seasonality) to the models. We also included the day since the beginning of the period (lockdown or not) to the model which could also account for seasonal affects. Moreover, in many cases we found a decrease in activity during the later no-lockdown period, negating a seasonality effect.

Our results picture a complex and dynamic urban ecological system where animal activity depends on species and site, as well as on environmental parameters and heterospecific (e.g., human) activity. This complexity might explain the contradicting effects of lockdown reported by others (Gordo et al., 2021; Estela et al., 2021; Schrimpf et al., 2021; Manenti et al., 2020). It points towards the importance of monitoring activity across geographical and environmental landscapes and of including representative parameters in statistical models. Accurate and automated methods to estimate bio-diversity are going to be essential for monitoring future effects of global changes.

Materials and methods

Study site, species and period

The study was conducted at 17 different sites around the Tel-Aviv city in Israel (Figure 1A and Supplementary Materials 2, 3, 4). The sites represent three different common habitats in this area: small parks, residential areas and roads. They were randomly selected so that they are more or less evenly distributed within the region of the study. We sampled four parks (sites 9, 10, 11, 15), seven roads (sites 7, 12, 13, 14, 16, 17, 18) and six residential sites (sites 3, 4, 5, 6, 8, 19). The device placed in a fifth park was stolen. We focused on three bird species that are common in this urban environment, i.e., Hooded crow, Rose-ringed parakeet and Graceful prinia. The vocalizations of these species are loud, highly repeatable and stereotypic (Figure 1B), making them beneficial for developing an automatic recognition algorithm which is based on template matching (see next paragraph).

Spreading over a two-month period, the first lockdown in which we performed our recordings had different levels of severity. In the beginning, the restriction were strictly enforced with traffic on the roads decreasing almost to zero and with severe limitations imposed on human activity including a curfew preventing people from moving more than 100 m from home. Use of the parks was also not allowed and accordingly, they were empty. Over time though, the enforcement was loosen and human activity gradually returned to normal until the official removal of the lockdown. Using acoustic monitoring and automatic identification of three bird species, we compared bird and human activity during lockdown to a short period immediately after lockdown assuming that changes in activity between these adjacent time periods might be attributed to the lockdown (rather than to other environmental factors). We also account for seasonality by including environmental parameters (e.g., ambient temperature) in our models.

Acoustic survey

For each sampled site, we installed one automatic recording device, Audiomoth (Hill et al., 2017), on a tree trunk or a hedge at 1.7-4 m above the ground. We set the recorders to record 30 seconds every 2 minutes (30 second of recording, 1.5 min of pause) continuously during day and night with a sampling frequency of 192 kHz. Recording was monitored in four time periods during spring 2020, the peak of birds breeding season. Lockdown was covered by three sampling

periods: 25.3.2020-9.4.2020 (15 days), 24.4.2020-3.5.2020 (10 days) and 7.5.2020-16.5.2020 (10 days), in correspondence to Israel's government lockdown policy and one sampling period with no lockdown policy 21.5.2020-30.5.2020 (10 days). We only sampled 10 days after the lockdown to minimize seasonal changes. We also controlled for the uneven lockdown/no lockdown sampling periods by randomly choosing five sub-samples of 10 lockdown days each, and comparing them to the no-lockdown period. Detailed sampling times for each site are provided in the Table S1-S2 in Supplementary material 1. This sampling generated an audio dataset of 388,080 files (30 seconds each).

Automatic acoustic identification and bird activity

Because we only focused on birds (whose call frequencies remain below 10 kHz), to ease file handling, all audio files were first resampled to 22.05 kHz before further analysis. We also high-pass filtered the files with a cutoff at 1 kHz to minimize the interference of low frequency noise. For each species we selected a very common syllable (Figure 1B) which is typically used for conspecific communication, mostly serving as alarm or attachment calls in *C. corone* and *P. krameri* and as territorial songs in *P. gracilis*. To build an automatic identifier, we first manually selected 138 syllables of *C. corone cornix*, 173 syllables of *P. krameri* and 140 syllables of *P. gracilis* from a worldwide citizen science database of bird recordings (xeno-canto; http://www.xeno-canto.org/). These syllables were used as acoustic templates. We then used spectrogram image cross-correlation to automatically classify sound recordings using Avisoft SASLab Pro 5.1 (R. Specht, Avisoft Bioacoustics, Glienicke, Germany). Spectrogram image cross-correlations is a method for measuring maximum similarity index between the spectrograms of the template and the recordings at different time shifts. The similarity index is a value ranging from 0 to 1, with 1 meaning that the two spectrograms are identical. The higher the similarity index, the higher the similarity between template and audio, and hence the higher the probability that the bird vocalization occurs in the recording. We set the identification threshold to 0.5, and then we manually scrutinized all files with vocalizations above this threshold to make sure that no calls were missed. This high threshold also ensured that we only used high Signal-to-Noise-Ration vocalizations as very weak vocalizations did not correlate with our templates.

We referred to each file (30 seconds long) as an 'event'. That is, if we detected a vocalization of one of the three focal species within the file – we considered this as one occurrence of that species. The daily number of events was then used as a proxy for activity in our models (below). Hence, we used three variables to quantify bird activity: (1) The daily number of audio files, which included bird vocalizations of a specific species, was used as a proxy for the daily activity of this species and (2) the daily coefficient of variance (the standard deviation divided by the mean) of the number of audio files estimated in 30 min bins as a proxy of activity variability. (3) We also tested another model in which we used the number of syllables (and not a binary 0/1 value) as the measurement of bird activity.

Vocalization analysis

Because our results showed that the ambient noise levels during no lockdown were higher than during lockdown (see Results section), we further investigated whether birds modified their vocalizations to mitigate noise interference. We measured two acoustic parameters: (1) To assess changes in calling intensity, we estimated the root mean square (RMS) sound pressure computed over a window defined by a threshold of 20 dB below the peak of the vocalization and (2) To estimate changes in song pitch, we estimated the peak frequency of the vocalizations, i.e., the frequency with maximum amplitude (kHz). Both parameters were estimated from spectrograms computed with the following parameters: Fast Fourier transform with a 512 window; a Hamming window and a 75% overlap between windows, resulting in a temporal resolution of 5.8 ms and a frequency resolution: 43 Hz. Vocalizations were analyzed using Avisoft SASLab Pro 5.1.

Environmental data

We estimated two environmental parameters in the study area: (1) the ambient temperature, (2) the ambient noise level. The environment temperature was obtained from the Israel Meteorological service (https://ims.gov.il/en). The temperature was recorded every 10 min. The average temperature of each day was used for the analysis. To estimate ambient noise, we used the average daily sound power as a proxy for ambient noise (at each site). For each bird species, we assessed the noise at the peak-frequency of its vocalization, thus estimating the relevant noise for the species (i.e., Hooded crow: 1,600 Hz; Rose-ringed parakeet: 4,000 Hz; Graceful prinia: 5,000 Hz).

Human activity

To quantify human activity, we ran a random forest classifier implemented using the "TreeBagger" Matlab function. Firstly, we randomly chose a set of 5,960 one second samples from the recording data. Samples from each of the 17 sites were used. In each site, samples were taken over a 24 hour period from a random day (from both lockdown and no lockdown periods). Secondly, the content of each of these 5,960 samples was identified by listening of one of us (Y. Hassin) and identifying the presence of one or more of human speech sounds. There were 1,294 speech samples and 4,666 samples without speech sounds. Third, the 5,960 samples were divided into a "training" set (80% of the samples) and a "test" set (20% of the samples). The balanced accuracy of the classifier was 75%. Notably, this is far above chance, but more importantly, the accuracy was the same for lockdown and non-lockdown periods so that the comparison between them was fair (and this was our main interest). Finally, we ran the classifier on all recordings and counted the number of speech sounds per 30 sec as a proxy for human activity. Note that this method assesses human pedestrian (and not car) activity.

Statistics

To assess the effects of predictor factors on activity, we run generalized linear mixed models (GLMM) with a Poisson family distribution using the function 'glmer' in the R package 'lmerTest' (Kuznetsova et al., 2017). We tested the following predictors: the lockdown status (yes/no), ambient temperature, ambient noise level, bird species (removed when analyzing each species separately), site category (road, park, residential), human activity and the following interactions: the lockdown status and bird species (removed when analyzing each species separately), the lockdown status and site category, the lockdown status and the count-down (the count-down variable represented the days from the beginning of each lockdown phase to account for temporal dependencies and to represent accumulated effects), the lockdown status and noise. Bird activity was used as the response variable, and the sampling site and sampling time were used as random effects.

In order to check the differences in activity for each site category during no lockdown and during lockdown for the specific bird-site combination, we performed Post-hocs using the 'emmeans' function from the emmeans package (Lenth et al., 2020). The effect size per parameter (e.g., temperature) was estimated in % by an exponentiation of the coefficient and examining the effect of a change of a single unit in the relevant parameter (e.g., one degree).

To assess the effects of predictor factors on activity variability, we used linear mixed models (LMM), using the function 'lmer' in the R package 'lmerTest' (Kuznetsova et al., 2017). The predictors and random variables were the same as for the GLMM. To assure a normal distribution of the residuals prior to fitting the LMM, the activity variability for Graceful prinia was ln transformed while the following parameters were Box-Cox transformed activity variability (of all species together, Hooded crow and Rose-ringed parakeet), the peak frequency and the ambient noise level.

For all models, to select the best model, we used the Akaike information criterion corrected for small sample size (AICc) using the function 'dredge' in the R package 'MuMIn' (Bartoń 2015). The model with the lowest AICc value indicates the best-fitting model. Differences among AIC values were calculated as follows: $\Delta i = AICi - AIC_{min}$.

Furthermore, ΔAICc > 2 between the first and the second best models is considered the gold standard for model selection (Burnham & Anderson 2002); therefore, multimodel inference was performed if AIC differences were ≤ 2, using the model.avg function in the package 'MuMIn' (Bartoń 2022). When several models were fit the data equally (AIC differences of less than 2) we report the average effect size of these models.

We ran several additional models in which the explained parameter was not bird activity. To examine changes in ambient noise during no lockdown and during lockdown, an LMM was used with ambient noise level as the explained variable, lockdown status and site category as fixed factors and the specific sites as a random effect. To explore changes in vocal amplitude and peak frequency during no lockdown and during lockdown for each bird species, we created a LMM including vocal amplitude and peak frequency as a dependent variable, lockdown status and noise levels as the independent variables, and sampling site and sampling time as a random effect. To assess changes in human activity during no lockdown and during lockdown, we ran a GLMM with the lockdown status, the site category and their interactions as explanatory fixed factors, and sampling site and sampling time were used as random variables. For all models, the level for statistical significance was set at $\alpha < 0.05$. All statistical tests were conducted in R v. 4.1.2 (R Core Development Team 2021).

Data availability

The datasets supporting this article have been uploaded as part of the electronic supplementary material. See supplementary material 7, 8.

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Competing interests

The authors state no conflict of interest.

Author contributions

Congnan Sun, data analysis, Funding acquisition, Validation, Visualization, Methodology, Writing - original draft; Yoel Hassin, data acquisition, data analysis; Arjan Boonman, data analysis; Assaf Shwartz, Writing - review and editing. Yossi Yovel, Conceptualization, Resources, Supervision, Funding acquisition, Validation, Investigation, Methodology, Project administration, Writing - original draft, Writing - review and editing

Table 1. Effects of predictor variables on birds' activity based on generalized and general linear mixed models (GLMM and LMM). Estimates were calculated in % per day for the following units: Temperature – per degree, Noise – per dB, Human activity – per 1 talking event, Lockdown related parameter – per existence of the lockdown (yes/no).

Species	Dependent variable	Predictors	Estimate	*z*	*p*	95% CI	Percent
All species	**Activity-** Number of events/day	(Intercept)	7.850	22.541	< 0.001	-	-
		Bird_species	-0.623	-84.742	**< 0.001**	-	46.367
		Lockdown_status	-0.404	-2.623	**0.009**	-	33.236
		Human_activity	-0.00001	-0.539	0.590	-	0.001
		Noise	-0.062	-20.625	**< 0.001**	-	6.012
		Temperature	0.045	4.194	**< 0.001**	-	4.649
		Site_category_residence	-0.739	-2.764	**0.006**	-	53.286
		Site_category_road	-0.923	-3.558	**< 0.001**	-	62.075
		Lockdown_status*Count_down	0.008	3.820	**< 0.001**	-	0.835
		Lockdown_status*Site_category_residence	-0.072	-3.435	**0.001**	-	7.294
		Lockdown_status*Site_category_road	0.094	4.074	**< 0.001**	-	10.447
		Lockdown_status*Noise	-0.007	-2.723	**0.006**	-	0.746
		Lockdown_status*Human_activity	0.0003	14.074	**< 0.001**	-	0.032
		Bird_species*Lockdown_status	0.253	29.155	**< 0.001**	-	31.379
	#Activity Variability- CV of the number of events/day	(Intercept)	-0.963	5.975	< 0.001	-1.282, -0.618	-
		Bird_species	0.208	16.877	**< 0.001**	**0.184, 0.233**	-
		Lockdown_status	0.565	4.238	**< 0.001**	**0.269, 0.839**	-
		Noise	0.025	8.554	**< 0.001**	**0.0198, 0.030**	-
		Site_category_residence	0.170	2.403	**0.016**	**0.030, 0.310**	-
		Site_category_road	0.224	3.238	**0.001**	**0.089, 0.361**	-
		Human_activity	-0.00004	1.150	0.250	-0.0001, 0.00003	-
		Temperature	-0.010	3.394	**0.001**	**-0.016, -0.004**	-
		Bird_species*Lockdown_status	-0.057	3.888	**< 0.001**	**-0.086, -0.028**	-
		Count_down*Lockdown_status	-0.001	1.503	0.133	-0.003, 0.0004	-
		Lockdown_status*Noise	-0.008	3.157	**0.002**	**-0.013, -0.003**	-
		Lockdown_status*Human_activity	-0.00005	1.308	0.191	-0.00018, 0.00003	-
		Lockdown_status*Site_category_residence	0.023	0.641	0.522	-0.048, 0.098	-
		Lockdown_status*Site_category_road	0.036	0.995	0.320	-0.042, 0.106	-
Hooded crow	**#Activity-** Number of events/day	(Intercept)	7.475	20.026	< 0.001	6.743, 8.206	-
		Lockdown_status	-0.647	4.508	**< 0.001**	**-0.928, -0.366**	47.639
		Noise	-0.045	12.324	**< 0.001**	**-0.052, -0.038**	4.400
		Site_category_residence	-0.790	2.374	**0.018**	**-1.443, -0.1386**	54.616
		Site_category_road	-0.738	2.284	**0.022**	**-1.372, -0.105**	52.193
		Human_activity	-0.0001	3.376	**0.001**	**-0.0002, -0.00004**	0.010
		Count_down*Lockdown_status	0.017	6.542	**< 0.001**	**0.012, 0.022**	1.749
		Lockdown_status*Site_category_residence	-0.064	2.288	**0.022**	**-0.119, -0.009**	6.385

		Lockdown_status*Site_category_road	0.221	7.606	**< 0.001**	**0.164, 0.278**	25.722
		Lockdown_status*Human_activity	0.0004	10.456	**< 0.001**	**0.0003, 0.0004**	0.042
		Lockdown_status*Noise	-0.002	0.682	0.495	-0.009, 0.0056	0.212
		Temperature	-0.009	0.645	0.519	-0.037, 0.019	0.959
	#**Activity ariability-** CV of the number of events/day	(Intercept)	-1.447	7.373	< 0.001	-1.827, -1.023	-
		Lockdown_status	0.889	5.473	**< 0.001**	**0.534, 1.217**	-
		Noise	0.033	9.604	**< 0.001**	**0.026, 0.040**	-
		Site_category_residence	0.293	2.958	**0.003**	**0.095, 0.486**	-
		Site_category_road	0.236	2.479	**0.013**	**0.048, 0.423**	-
		Human_activity	0.00004	0.999	0.318	-0.00005, 0.0001	-
		Lockdown_status*Noise	-0.015	4.618	**< 0.001**	**-0.021, -0.008**	-
		Lockdown_status*Human_activity	-0.0001	2.959	**0.003**	**-0.0002, -0.00005**	-
		Temperature	-0.003	1.074	0.283	-0.010, 0.003	-
		Count_down*Lockdown_status	-0.001	1.032	0.302	-0.003, 0.001	-
		Lockdown_status*Site_category_residence	0.045	1.000	0.317	-0.0414, 0.141	-
		Lockdown_status*Site_category_road	-0.009	0.204	0.838	-0.095, 0.082	-
Rose-ringed parakeet	#**Activity-** Number of events/day	(Intercept)	6.320	11.848	< 0.001	5.272, 7.373	-
		Lockdown_status	-0.106	0.379	0.704	-0.656, 0.443	10.058
		Noise	-0.061	10.900	**< 0.001**	**-0.072, -0.050**	5.918
		Site_category_residence	-0.493	1.175	0.240	-1.314, 0.329	38.921
		Site_category_road	-1.201	2.949	**0.003**	**-1.999, -0.403**	69.911
		Human_activity	-0.0003	6.891	**< 0.001**	**-0.0004, -0.0002**	0.030
		Temperature	0.060	3.990	**< 0.001**	**0.031, 0.089**	6.307
		Lockdown_status*Noise	-0.016	3.268	**0.001**	**-0.026, -0.006**	1.635
		Lockdown_status*Site_category_residence	0.408	9.968	**< 0.001**	**0.328, 0.488**	52.396
		Lockdown_status*Site_category_road	0.574	13.488	**< 0.001**	**0.491, 0.658**	81.412
		Lockdown_status*Human_activity	0.001	15.304	**< 0.001**	**0.0006, 0.0008**	0.106
		Count_down*Lockdown_status	0.004	1.234	0.217	-0.002, 0.011	0.429
	#**Activity ariability-** CV of the number of events/day	(Intercept)	-0.460	3.225	0.001	-0.751, -0.178	-
		Lockdown_status	0.249	2.775	**0.006**	**0.065, 0.442**	-
		Noise	0.020	8.303	**< 0.001**	**0.015, 0.025**	-
		Site_category_residence	0.090	1.054	0.292	-0.078, 0.256	-
		Site_category_road	0.196	2.376	**0.018**	**0.032, 0.357**	-
		Human_activity	0.00001	0.419	0.675	-0.00005, 0.00007	-
		Temperature	-0.007	2.331	**0.020**	**-0.012, -0.001**	-
		Count_down*Lockdown_status	-0.003	4.333	**< 0.001**	**-0.005, -0.002**	-
		Lockdown_status*Site_category_residence	-0.051	1.818	0.069	-0.105, 0.005	-
		Lockdown_status*Site_category_road	-0.109	3.915	**< 0.001**	**-0.164, -0.053**	-
		Lockdown_status*Human_activity	-0.0001	3.108	**0.002**	**-0.0002, -0.00004**	-
		Lockdown_status*Noise	-0.002	0.866	0.387	-0.008, 0.0033	-

Graceful prinia	**Activity-** Number of events/day	(Intercept)	3.314	2.245	0.025	-	-
		Lockdown_status	-0.352	-0.595	0.552	-	29.672
		Human_activity	0.00017	2.367	**0.018**	-	0.017
		Noise	-0.165	-17.114	**< 0.001**	-	15.211
		Temperature	0.365	6.533	**< 0.001**	-	44.051
		Site_category_residence	-1.012	-1.440	0.150	-	64.287
		Site_category_road	-1.484	-2.164	**0.030**	-	78.874
		Lockdown_status*Count_down	-0.104	-14.979	**< 0.001**	-	10.174
		Lockdown_status*Site_category_residence	-0.062	-1.159	0.247	-	6.252
		Lockdown_status*Site_category_road	-1.203	-13.290	**< 0.001**	-	73.469
		Lockdown_status*Noise	0.066	7.072	**< 0.001**	-	7.232
		Lockdown_status*Human_activity	0.003	3.513	**< 0.001**	-	0.300
	#**Activity ariability-** CV of the number of events/day	(Intercept)	0.920	1.496	0.135	-0.284, 2.100	-
		Lockdown_status	-0.194	0.655	0.513	-0.782, 0.425	-
		Noise	0.018	1.823	0.068	-0.002, 0.038	-
		Site_category_residence	0.210	0.946	0.344	-0.227, 0.643	-
		Site_category_road	0.556	2.452	**0.014**	**0.117, 1.009**	-
		Temperature	-0.031	2.592	**0.010**	**-0.054, -0.007**	-
		Count_down*Lockdown_status	0.005	1.578	0.115	-0.001, 0.011	-
		Lockdown_status*Site_category_residence	0.172	1.461	0.144	-0.058, 0.406	-
		Lockdown_status*Site_category_road	0.274	2.089	**0.037**	**0.0163, 0.532**	-
		Lockdown_status*Noise	-0.005	0.403	0.687	-0.029, 0.020	-
		Human_activity	-0.00004	0.437	0.662	-0.0003, 0.0002	-
		Lockdown_status*Human_activity	0.00007	0.394	0.694	-0.0003, 0.0004	-

CV: coefficient of variance. *: Interaction effect. 95% confidence intervals of the parameters that did not overlap zero are indicated in bold. #: model average.

Table 2. Effects of predictor variables on the root mean square (RMS) and peak frequency in three bird species based on the linear mixed models (LMM).

Species	Dependent variable	Predictors	Estimate	*t*	*p*
Hooded crow	RMS	Lockdown_status	0.064	0.148	0.883
		Noise	0.354	7.054	**< 0.0001**
	Peak frequency	Lockdown_status	-5.99E-04	-0.601	0.552
		Noise	9.17E-05	0.728	0.468
Rose-ringed parakeet	RMS	Lockdown_status	1.065	3.290	**0.001**
		Noise	0.470	7.772	**< 0.0001**
	Peak frequency	Lockdown_status	3.93E-03	3.235	**0.001**
		Noise	1.34E-04	0.783	0.435
Graceful prinia	RMS	Lockdown_status	0.208	0.475	0.635
		Noise	0.844	9.449	**< 0.0001**
	Peak frequency	Lockdown_status	1.31E-04	0.083	0.935
		Noise	2.40E-03	0.928	0.357

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Supplemental materials

Supplementary material 1——

Table S1. The sampling time and lockdown status for each site

Table S2. The latitude and longitude of the sampling site

Table S3. The sampling time and daily number of audio files including crow's vocalizations for each site

Table S4. The sampling times and daily number of audio files including parakeet's vocalizations for each site

Table S5. The sampling times and daily number of audio files including prinia's vocalizations for each site

Supplementary material 2——The activity of hooded crow at 17 sites in central Tel-Aviv

Supplementary material 3——The activity of rose-ringed parakeet at 17 sites in central Tel-Aviv

Supplementary material 4——The activity of graceful prinia at 17 sites in central Tel-Aviv

Supplementary material 5——

Figure S1. The ambient noise level **(**dB**)** between no lockdown period and lockdown period

Figure S2–**S6.** Activity of birds. Boxplots show the activity of (A) Human activity, (B) Hooded crow, (C) Rose-ringed parakeet, and (D) Graceful prinia for each site category during no lockdown and during lockdown. Green box plot: park; Grey box plot: road; Blue box plot: residence; Black box plot: overall. Note that human activity was assessed based on human speech so the increase observed during lockdowns in roads represents pedestrian and not car activity. Box plot lower and upper box boundaries show the 25th and 75th percentiles, respectively, with the median inside. The lower and upper error lines depict the 10th and 90th percentiles, respectively. Outliers of the data are shown as black dots. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

Figure S7. Activity of birds. Boxplots show the activity of (A) all species, (B) Hooded crow, (C) Rose-ringed parakeet, and (D) Graceful prinia for each site category during no lockdown and during lockdown. Green box plot: park; Grey box plot: road; Blue box plot: residence; Black box plot: overall. Box plot lower and upper box boundaries show the 25th and 75th percentiles, respectively, with the median inside. The lower and upper error lines depict the 10th and 90th percentiles, respectively. Outliers of the data are shown as black dots. Asterisks indicate significant differences between no lockdown and lockdown periods. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Activity is defined as the daily number of syllables of bird vocalizations per day. Different sampling sites represented by different symbols.

Table S6. Results from generalized linear mixed models (GLMM) comparing the differences in human activity between no lockdown period and lockdown period for all sites and for each site.

Table S7. Akaike's information criterion (AICc) model comparison results for activity and activity variability in all species and each bird species.

Table S8. Results from post hoc tests comparing the differences in activity and activity variability between no lockdown period and lockdown period in all species for each site. Estimates were calculated in % per day for the following units: Temp – per degree, Noise – per dB, Human activity – per 1 talking event, Lockdown related parameter – per existence of the lockdown (yes/no).

Table S9. Akaike's information criterion (AICc) model comparison results for activity and activity variability in all species and each bird species.

Table 10. Effects of predictor variables on birds' activity based on generalized and general linear mixed models (GLMM and LMM). Estimates were calculated in % per day for the following units: Temperature – per degree, Noise – per dB, Human activity – per 1 talking event, Lockdown related parameter – per existence of the lockdown (yes/no).

Table S11. Results from post hoc tests comparing the differences in activity and activity variability between no lockdown period and lockdown period in all species for each site. Estimates were calculated in % per day for the following units: Temp – per degree, Noise – per dB, Human activity – per 1 Human_activitying event, Lockdown related parameter – per existence of the lockdown (yes/no).

Supplementary material 6——

Table S12. The sampling time and daily number of syllables including crow's vocalizations for each site

Table S13. The sampling times and daily number of syllables including parakeet's vocalizations for each site

Table S14. The sampling times and daily number of syllables including prinia's vocalizations for each site

Supplementary material 7——The activity datasets supporting this article

Supplementary material 8——The acoustic datasets supporting this article

Supplementary movie S1——Dynamic illustrations of the changes in crow's activity

Supplementary movie S2——Dynamic illustrations of the changes in parakeet's activity

Supplementary movie S3——Dynamic illustrations of the changes in prinia's activity