

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, 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 and 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 depended on many environmental parameters and 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.

eLife assessment

This manuscript offers a **valuable** contribution to studying wildlife responses during and after COVID-19 lockdowns. It **convincingly** demonstrates that bird species in urban areas respond differently to human activity changes. What sets this study apart from others on avian responses to COVID-19 lockdowns is its use of passive acoustic monitoring. By concurrently measuring anthropogenic noise, a crucial reflection of changes in human activity due to COVID-19 lockdowns, this study reveals rare local-scale variations in bird responses to human activity. Only one study so far has used vocalization recordings to assess the effects of COVID-19 lockdowns on a bird species.

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 lockdowns (Vardi et al., 2021 [↗](#)). Several studies reported an increase in avian abundances in urban habitats (Schrimpf et al., 2021 [↗](#)), while other studies 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 were performed in large scale with widely spread sampling points, and 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 fine-scale studies to explore how species with different levels of adaptation to human activity were affected by the lockdowns across habitats neighboring one-another. Such research can help advancing 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 affected by 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 allows 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. An 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, allowing to evaluate the impact of local human disturbance on species (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 standardized manner.

In this study we aimed to examine the effects of the Covid 19 lockdown on the activity of 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 environments 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 and developed environments. These species together with non-native invasive alien species that have also adapted to exploit various anthropogenic 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 these 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 its main habitat. The first two species can be considered as urban exploiters or synanthropic species that thrive in urban areas, and their population is increasing in Israel, while the third one represents an urban adaptor with a population that is currently decreasing in Tel-Aviv and across the country (Colléony & Shwartz 2020 [↗](#)). All birds were within their breeding season during both the lockdown and non-lockdown periods (Methods).

We performed our study around the first lockdown period in Israel (March-May 2020). We selected common vocalizations emitted by each species usually in intra-specific contexts (see Methods). To reduce the effect of ambient noise on our findings, we focused on loud vocalizations that were high above the noise level. 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 all within the urban environment of central Tel-Aviv on average ~200 m apart from each other. Thus, our sampling was much denser than most previous studies allowing us to examine changes over fine spatial scales. 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 (the Yarkon Park), recognized as an important bird resource in Tel-Aviv and servicing as green corridor connecting the city to more natural environments around it (Figure 1A [↗](#); Shwartz et al., 2008 [↗](#)).

We quantified birds' presence and found changes in bird activity during the lockdown period that were species and habitat specific. We found that human following (exploiter) species probably moved their activity to residential areas during the lockdown, in contrast to a human aversive species (an adapter) that seemingly increased its activity in all habitats in the absence of humans. Other environmental factors, such as ambient temperature, also influenced bird activity, but the

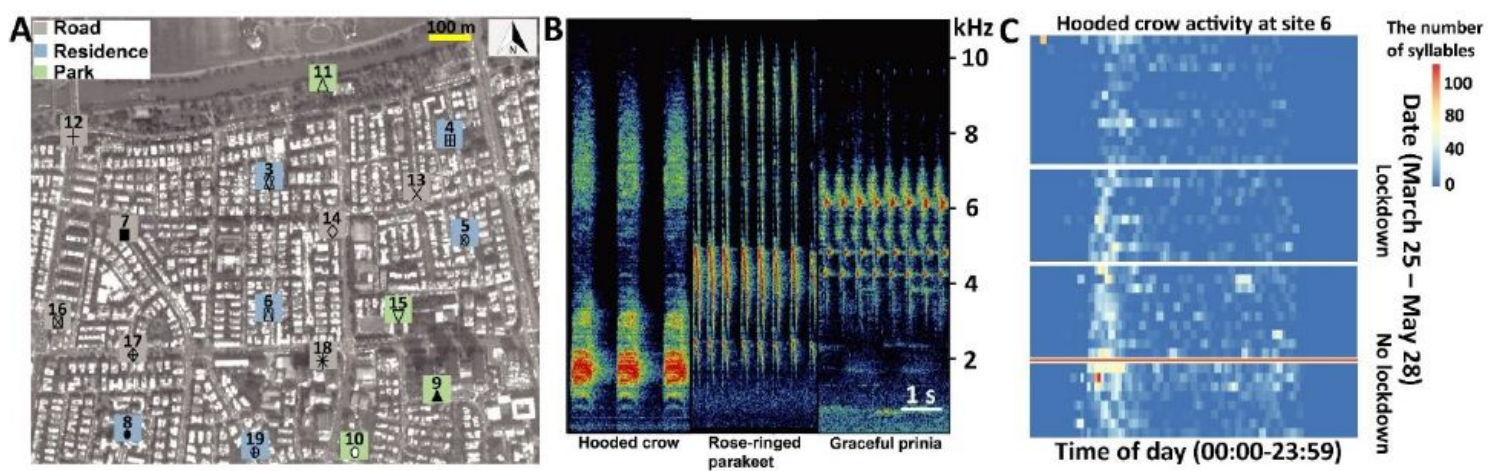


Figure 1.

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.

effect of the lockdown was central even after controlling for these variables. 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.

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. In addition, human activity significantly increased in residential areas by 49% during the lockdown and significantly decreased in parks by 31% as visiting parks was forbidden as expected (**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 than during the non-lockdown period 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 not enough to explain changes in bird activity during 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

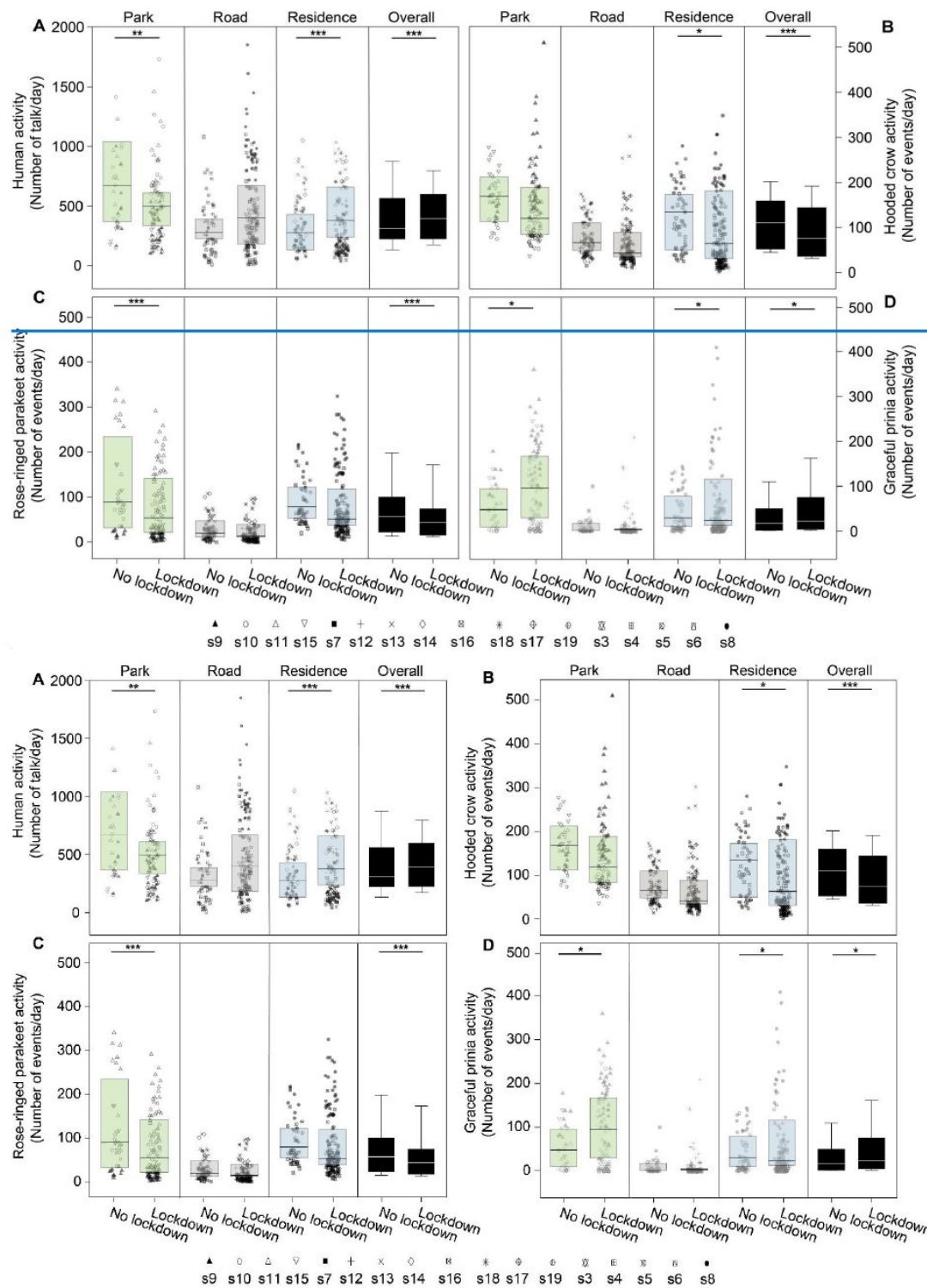


Figure 2.

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. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

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
	#Activity ariability- CV of the number of events/day	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
		(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	-
Rose-ringed parakeet	#Activity- Number of events/day	Lockdown_status*Site_category_road	-0.009	0.204	0.838	-0.095, 0.082	-
		(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 prima	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 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).

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, the 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 significant (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).

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); This approach was chosen over taking the last 10 days of the lockdown period, because towards the end of the lockdown, its enforcement was loosened and people gradually returned to their normal (pre-lockdown) behavior. (2) we performed a permutation test where we permuted the lockdown status of each day (while maintaining the number of lockdown and no-lockdown 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.

To assess the relative importance of the various parameters which contributed to the best explanatory model, we used the parameters of the best model (site category, ambient noise, human activity, temperature and lockdown status) and ran a discriminant function analysis (DFA) aiming to classify the level of bird activity (see Methods). The DFA's managed to significantly classify bird activity for all three species (62.7% for Hooded crows, 80.7% for Rose-ringed parakeets and 82.5% for Gracefull prinias (binomial test: $P < 0.001$ and see Table S9 for the full details)). Analyzing the result showed that the first discriminant function explained a great majority of the variance and that it was affected (almost equally) by all for five parameters in a species-specific manner (see Table S9).

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 suggest that this apparent increase was probably 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**, note that all slopes are ≤ 1 ; 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 significantly lower peak frequencies during lockdown, but the difference was negligible: ~ 4 Hz, **Table 2**).

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). Several reports however demonstrated that these claims may have been exaggerated, and that species different responded differently to the sudden changes in human activity (Vardi et al., 2021). Yet, fine empirical evidence on how species activity changed during lockdown is scarce and knowledge is important to further understand how wildlife respond to human activity (Montgomery et al., 2021). Our fine-scale continuous acoustic monitoring of bird activity during lockdown and no-lockdown periods in various urban environments 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 songbird, 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 but that they might depend on the specific habitat and also rely on many additional ambient parameters.

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 to changes in noise or temperature as these were accounted for in the models (but note that we used linear models and thus might have not fully accounted for them). Human presence (assessed by detecting human speech) could also not fully explain the shifts we observed in bird activity. Indeed, the activity of all species significantly correlated with human presence, but the presence of humans did 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 the latter. It is likely that additional factors that were altered by the lockdown such as the specific type of human activity (e.g., jogging and littering vs. walking) affected the birds' decision of activity. We also note

Species	Dependent variable	Predictors	Estimate	<i>t</i>	<i>p</i>
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

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).

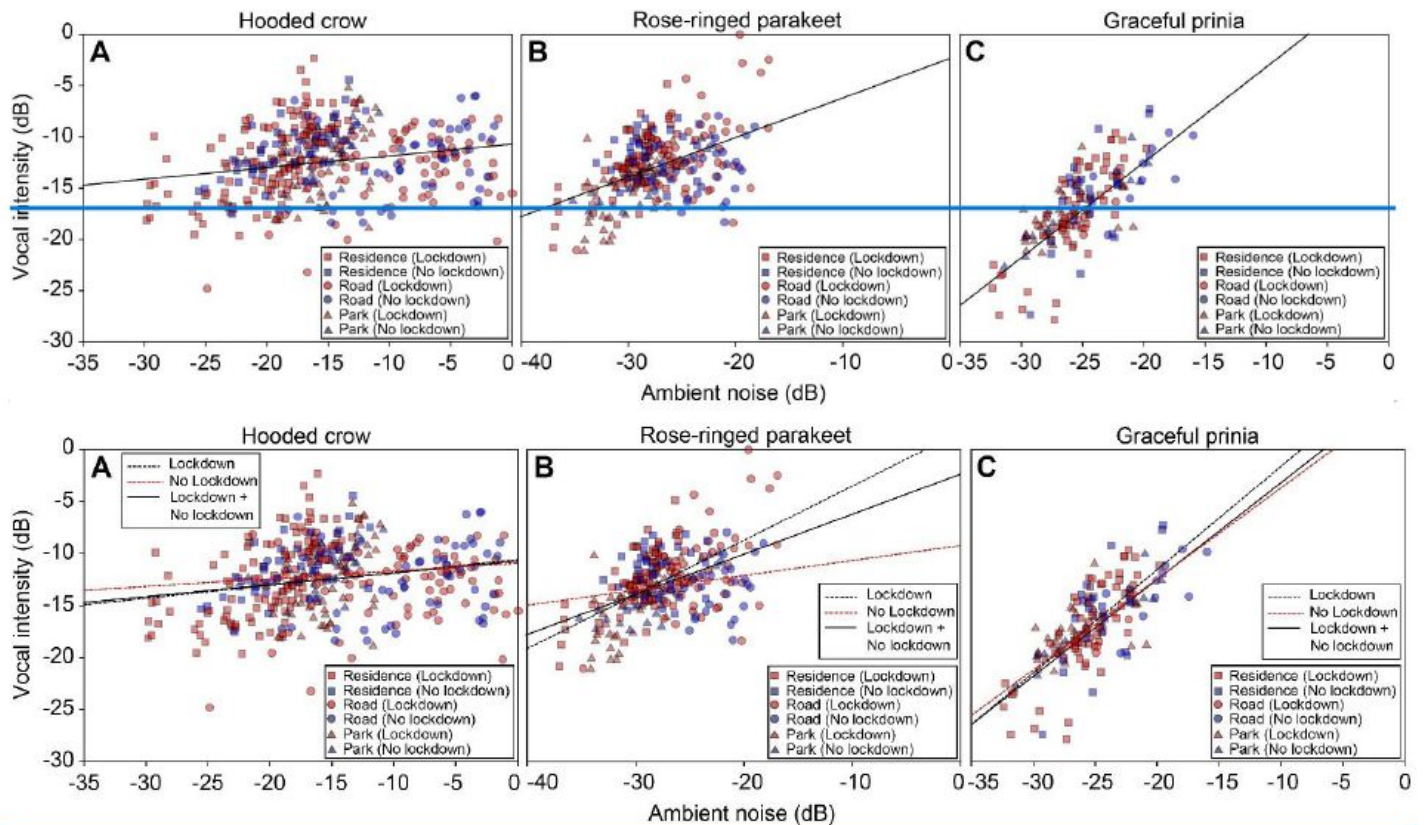


Figure 3.

Vocal intensity as a function of ambient noise (normalized to maximum) for (A) Hooded crows. (B) Rose-ringed parakeets and (C) Graceful prinia. 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. The lines represent regression lines (solid line: Lockdown and No lockdown together; black dashed line: Lockdown; red black dashed line: No lockdown). The equations of the linear fits: $y = 0.124x - 10.554$ (Hooded crow; Lockdown); $y = 0.075x - 10.877$ (Hooded crow; No lockdown); $y = 0.521x + 1.705$ (Rose-ringed parakeet; Lockdown); $y = 0.143x - 9.204$ (Rose-ringed parakeet; No lockdown); $y = 0.993x + 8.354$ (Graceful prinia; Lockdown); $y = 0.876x + 5.110$ (Graceful prinia; No lockdown).

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. Thus, the last days of the lockdown period might have been more similar to the no-lockdown periods, weakening our results.

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, e.g., birds might be more or less vocal due to human activity without changing their position. We tried 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 (mostly in flight) 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 territorial male songs, typically uttered towards conspecifics, 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 the Tel-Aviv area 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 a significant change in bird vocal acoustics during the lockdown periods. Specifically, we observed an increase in vocalization amplitudes that was less than the increase in ambient noise. An increase in noise (at the same frequency band as the vocalization) will (by definition) increase the measured amplitudes of the vocalization making it impossible to detect a real increase in vocal intensity, unless the increase is larger than the increase in noise. Birds thus might have increased vocal intensity (minutely), but this could not have been detected using our method. Other studies that controlled for the recording distance (e.g., Derryberry et al., 2020 [↗](#)) did find a change in intensity but this should not have affected our results regarding the frequency.

Various decisions must be made when using acoustic monitoring, such as when 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 S10-S12 in Supplementary material 5). The distribution of the birds' syllables along the sampling periods can be found in Table S13-S15 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. This also reduced the risk that our results were caused by a change in bird distribution in the area around the microphone (e.g., the birds were close or farther from the microphones). Moreover, if our findings were a result of birds escaping the presence of humans, we would have expected to see a large effect of human activity in the models, which was not the case. Finally, for some bird species, acoustic monitoring could also allow to distinguish between various behaviors, but we did not apply this approach here. Importantly, 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 three degrees. To control for this, we added temperature (which is a proxy of seasonality) to the models. We also tested a model where the five days with extremely high temperatures were removed but the results did not change (see Table S16-S17 in Supplementary material 5). We also included the day since the beginning of the period (lockdown or not) to the model which could also account for seasonal effects. Moreover, in many cases we found a decrease in activity during the later no-lockdown period, excluding the possibility that all our results could be explained by a seasonal 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. We moreover demonstrate that bird activity patterns can differ on a local scale only hundreds of meters apart. This complexity might explain the contradicting effects of lockdown reported by others ([Gordo et al., 2021](#); [Estela et al., 2021](#); [Schrumpf et al., 2021](#); [Manenti et al., 2020](#)). It points towards the importance of monitoring activity in fine-scale across geographical and environmental landscapes and of including environmental parameters in statistical models. Accurate and automated long-term methods to estimate bio-diversity done in parallel to environmental measurements 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 in Tel-Aviv, 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 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). A 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 rather easy for automatic recognition based on template matching (see next section).

Spreading over a two-month period, the first lockdown in which we performed our recordings had different levels of severity. In the beginning, the restrictions 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 loosened, 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. It is important to note that all recordings were made during the breeding season of the three species. We would like to note that in terms of breeding, all birds were within the same state during both the lockdown and the non-lockdown periods. Parakeets and crows have a long breeding season Feb-end of June with one cycle. They will stay around the nest throughout this season and especially in the peak of the season March-May. Prinias start slightly later at the beginning of March with 2-3 cycles till end of June.

Acoustic survey

At each site, we installed one recording device, Audiomoth (Hill et al., 2017), on a tree trunk or a hedge at 2-4 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 performed in 4 time-bouts during spring 2020, the peak of birds breeding season. Three of the sampling periods were during the lockdown: 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) and one sampling period was immediately after the removal of the lockdown 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. This sampling generated an audio dataset of 388,080 files (30 seconds each). Detailed sampling times for each site are provided in Table S1-S2 in Supplementary material 1.

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 (following low-pass-filtering to avoid aliasing). We also high-pass filtered the files with a cutoff at 1 kHz to minimize the interference of low frequency noise (this was not applied when estimating ambient 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 between the spectrograms of the template and the recordings at different time shifts. The output similarity index is a value ranging from 0 to 1. The higher the similarity index, the higher the similarity between template and audio (with 1 meaning that the two spectrograms are identical), 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 high-quality 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 total number of syllables per file (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). We also examined another noise parameter where the noise was estimated as the power under 1kHz for all species but this did not alter the results (see Table S18-S19 in Supplementary material 5).

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 (taken from all sites). In each site, samples were taken over a 24 hour period from a random day (from both lockdown and no lockdown periods). Second, the content of each of these 5,960 samples was identified by listening and identifying the presence of human speech sounds. In total, there were 1,294 speech samples and 4,666 samples without speech. 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 while the noise measurement (previous section) refers to car noise.

Discriminant Function Analysis

DFA analysis was run in SPSS v20.0 (SPSS Inc., Chicago, IL, U.S.A.) using a leave-one-out-cross-validation procedure. Activity was normalized across sites to a range between 0-1 and we defined 5 levels of activity 0-0.2, 0.2-0.4, 0.4-0.6, 0.6-0.8 and 0.8-1.0 The success of the DFA was determined with a binomial test comparing the DFA's classification performance to a random classification (i.e., chance level of 20%). The prior probabilities of the DFA classes were adjusted to be equal.

Statistics

To assess the effects of different predictor factors on activity, we run generalized linear mixed models (GLMM) with a Poisson 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, 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 between the no lockdown and lockdown periods for the specific bird-site combinations, 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: $\Delta_i = AIC_i - AIC_{min}$. Furthermore, $\Delta AICc > 2$ 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 between the no lockdown and lockdown periods, a LMM was used with ambient noise 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 between the no lockdown and lockdown periods for each bird species, we created an LMM using either vocal amplitude or peak frequency as the explained variable, the lockdown status and noise levels as the independent variables, and sampling site and sampling time as random effects. To assess changes in human activity between the no lockdown and lockdown periods, we ran a GLMM with the lockdown status, the site category and their interactions as explanatory fixed factors, and the sampling site and sampling time as random effects. 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 Schwartz, Writing - review and editing. Yossi Yovel, Conceptualization, Resources, Supervision, Funding acquisition, Validation, Investigation, Methodology, Project administration, Writing - original draft, Writing - review and editing

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.

Figure S8. The examples of different types of noise. (A)-(C) Car noise; (D) Motorcycle noise. Oscillograms (above), power spectrum (left) and spectrograms (below).

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. Assessment of model fit of the discriminant function analyses on the parameters of the best model in three bird species.

Table S10. Akaike's information criterion (AICc) model comparison results for activity and activity variability in all species and each bird species.

Table S11. 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 S12.** 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_activating event, Lockdown related parameter – per existence of the lockdown (yes/no).

Table S16. 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 S17.** Akaike's information criterion (AICc) model comparison results for activity and activity variability in all species and each bird species.

Table S18. 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 S19.** Akaike's information criterion (AICc) model comparison results for activity and activity variability in all species and each bird species.

Supplementary material 6——

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

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

Table S15. 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

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Reviewer #1 (Public Review):

Summary:

This study is one of several around the world to investigate how urban wildlife responded to changes in human activity during the lockdowns associated with the COVID-19 pandemic. Unlike several other studies on the topic that used observational data from citizen science programs, this project relied on passive acoustic monitoring to record bird vocalizations during and after stringent lockdown periods in an urban environment. The authors focused on three species that differ in their level of adaptation to human presence, providing an

ecologically relevant comparison that highlights the importance of micro-habitats for species living in close proximity to humans.

Strengths:

The element that sets this study apart from most others examining avian responses to COVID-19 lockdowns is the use of passive acoustic monitoring. As the authors describe, this method offers several advantages over other methods (though, it does come with some limitations on what questions can be addressed). Perhaps the most relevant advantage is that it offers the ability to concurrently measure anthropogenic noise in the environment, which is one of the most likely mechanisms for effects on wildlife from changes to human activity. These authors were, therefore, able to show local-scale differences in bird responses to human activity measured at the same scale. To my knowledge, only one other study (Derryberry et al. Science. 2020) has used recordings of vocalizations to examine the influence of COVID-19 lockdowns on a bird species.

It was encouraging to see a study that focused on the local-scale impacts of lockdowns, with methods that could investigate effects within micro-habitats. Logistics prevented many other projects from operating at such fine scales, making the results from this study particularly useful for the examination of rapid changes in bird behavior. This does mean that comparisons between this study and others examining the effects of COVID-19 lockdowns on birds should be done with care, as the effects described here may have been the result of different processes, operating at different spatial and temporal scales. However, that also means this study fills an important gap in our knowledge of how wildlife reacts to human activity in urban spaces.

Weaknesses:

One drawback of the approach is that the acoustic sampling only occurred during the pandemic: samples were taken during several lockdown periods in the early spring (March through early May) of 2020 and then for a period of 10 days after the end of the final lockdown period in late May of 2020. Unfortunately, this means that the interpretation of the effect of lockdowns could have been affected by any shifts in the birds' vocal behavior that resulted from unmodeled environmental factors or normal seasonal phenology during that three-month period. However, the authors chose focal species that would be less prone to seasonal changes in vocal behavior and their approach did account for several factors to minimize any such effects.

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Reviewer #2 (Public Review):

In this study, the authors tried to gauge the effect of human activity on three species, (1) the Hooded grow, an urban exploiter, (2) the Rose ring 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. A goal of the study was to increase awareness of the importance of urban parks.

Strengths:

Strengths of the study include the fact that it was conducted at 17 different sites, including parks, roads and residential areas, and included three species with different habitat preferences. Each species produced relatively loud and repeatable vocalizations. To avoid the effect of seasonal changes, sounds were sampled within a 10 day period of the lockdown as well as post-lockdown. The analysis included a comparison of the number of sound files, binary values indicating emission of a common syllable, and also the total number of

syllables emitted as a measurement of bird activity. Ambient temperatures and sound levels of human activity were also recorded. All of these factors speak to the comprehensive approach and analysis adopted in this study. The results are based on a rigorous statistical analysis, ruling out the effects of various extraneous parameters.

Weaknesses:

Most significant changes may occur near the ambient noise levels and this could lead to a different conclusion, but the authors acknowledge this possibility and clarify that they only analyzed vocalizations with high signal-to-noise signals to avoid ambiguity. In the revised version, they also replaced the previous ambient noise parameter with an estimate of ambient noise under 1kHz, assuming that it reflects most anthropogenic noise (not restricted to human speech). This seems reasonable and this new model gave very similar results to the previous one.

In interpreting the data, the authors mention the effect of human activity on bird vocalizations in the context of inter-species predator-prey interactions; however, the presence of humans could also modify intraspecies interactions by acting as triggers for communication of warning and alarm, and/or food calls (as may sometimes be the case) to conspecifics. The behavioral significance of the syllables used to monitor animal activity could be informative in this context; however, the authors acknowledge this possibility in the Discussion. Most importantly, the authors acknowledge the possibility of the above-noted bias, and the potential of a transient nature of the observed effects.

Conclusion:

In general, the authors achieved their aim of illustrating the complexity of the affect of human activity on animal behavior notwithstanding the caveats noted above. Their study also makes it clear that estimating such affects is not simple given the dynamics of animal behavior. For example, seasonality, temperature changes, animal migration and movement, as well as interspecies interactions, such as those related to predator-prey behavior, and inter/intra-species competition in other respects can all play into site-specific changes in the vocal activity of a particular species.

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Author Response

The following is the authors' response to the current reviews.

We confirm that that “count-down” parameter, mentioned by reviewer 1, is indeed counted from the first lockdown day and increases continuously, even when we do not have any data – and that this is clearly written in the manuscript.

The following is the authors' response to the original reviews.

Reviewer 1:

(Note, while these authors do reference Derryberry et al., I thought that there could have been much more direct comparison between the results of the two approaches).

We added some more discussion of the differences between the papers.

One important drawback of the approach, which potentially calls into question the authors' conclusions, is that the acoustic sampling only occurred during the pandemic: for several lockdown periods and then for a period of 10 days immediately after the end of the final lockdown period in May of 2020. Several relevant things changed from March

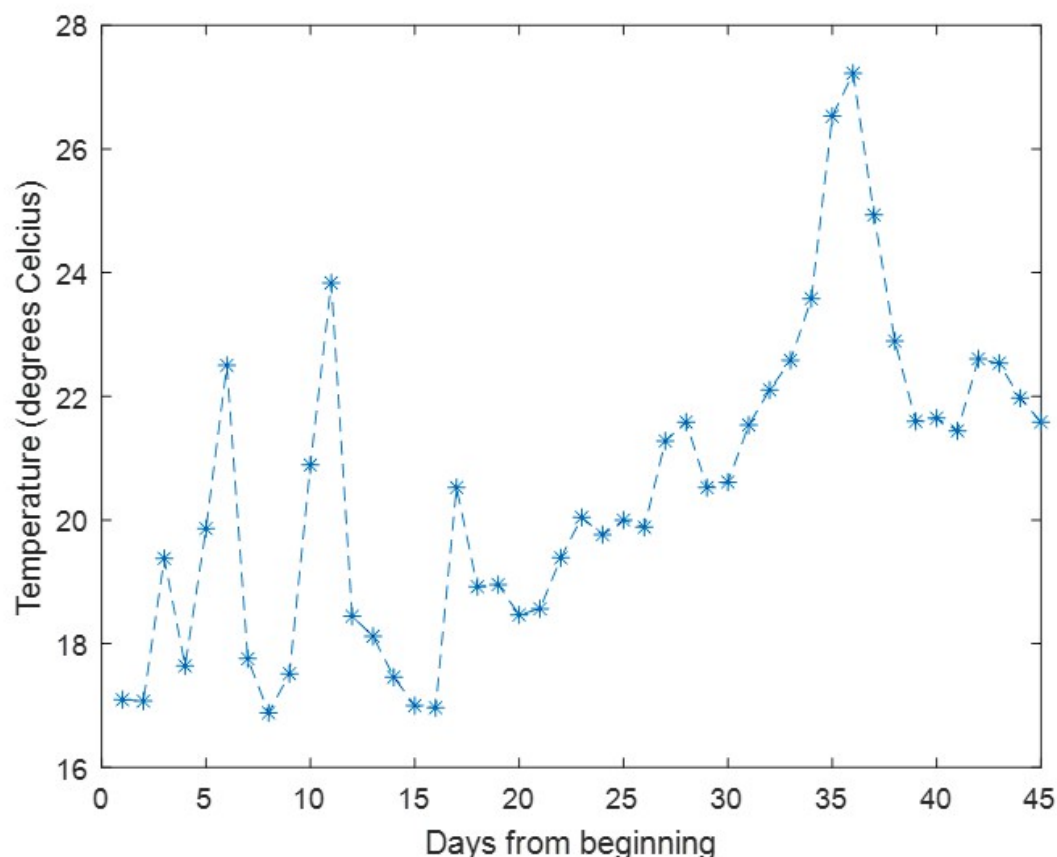
to May of 2020, most notably the shift from spring to summer, and the accompanying shift into and through the breeding season (differing for each of the three focal species). Although the statistical methods included an attempt to address this, neither the inclusion of the "count down" variable nor the temperature variable could account for any non-linear effects of breeding phenology on vocal activity. I found the reliance on temperature particularly troubling, because despite the authors' claims that it was "a good proxy of seasonality", an examination of the temperature data revealed a considerable non-linear pattern across much of the study duration. In addition, using a period immediately after the lockdowns as a "no-lockdown" control meant that any lingering or delayed effects of human activity changes in the preceding two months could still have been relevant (not to mention the fact that despite the end of an official lockdown, the pandemic still had dramatic effects on human activity during late May 2020).

In general, the reviewer is correct, and we reformulated some of the text to more carefully address these points. However, we would like to note two things: (1) Changes occurred rapidly with birds rapidly changing their behavior – this is one of the main conclusions of our study, i.e., that urban dwelling animals are highly plastic in behavior. So that lingering effects were unlikely. (2) Changes occurred in both directions, and thus seasonality (which is expected to have a uni-directional effect) cannot explain everything we observed. We are not sure what the reviewer means by ‘considerable non-linear patterns’ when referring to the temperature. Except for ~5 days with temperatures that exceeded the expected average by 3-4 degrees, the temperature increased approximately linearly during the period as expected from seasonality (see Author response image 1). Following the reviewer’s comment, we tested whether exclusion of data from these days changes the results and found no change.

We would like to note that in terms of breeding, all birds were within the same state during both the lockdown and the non-lockdown periods. Parakeets and crows have a long breeding season Feb-end of June with one cycle. They will stay around the nest throughout this season and especially in the peak of the season March-May. Prinias start slightly later at the beginning of March with 2-3 cycles till end of June.

Regarding the comment about human activity, as we now also note in the manuscript, reality in Israel was actually the opposite of the reviewer’s suggestion with people returning to normal behavior towards the end of the lockdown (even before its official removal). We believe that this added noise to our results, and that the effect of the lockdown was probably higher than we observed.

Author response image 1.



Another weakness of the current version of the manuscript is the use of a supposed "contradiction" in the existing literature to create the context for the present study. Although the various studies cited do have many differences in their results, those other papers lay out many nuanced hypotheses for those differences. Almost none of the studies cited in this manuscript actually reported blanket increases or decreases in urban birds, as suggested here, and each of those papers includes examples of species that showed different responses. To suggest that they are on opposite sides of a supposed dichotomy is a misrepresentation. Many of those other studies also included a larger number of different species, whereas this study focused on three. Finally, this study was completed at a much finer spatial scale than most others and was examining micro-habitat differences rather than patterns apparent across landscapes. I believe that highlighting differences in scale to explain nuanced differences among studies is a much better approach that more accurately adds to the body of literature.

We thank the reviewer for this good feedback and revised the manuscript, accordingly, placing more emphasis on the micro-scale of this study.

Finally a note on L244-247: I would recommend against discounting the possibility that lockdowns resulted in changes to the birds' vocal acoustics, as Derryberry et al. 2020 found, especially while suggesting that their results were the effects of signal processing artifacts. Audio analysis is not my area of expertise, but isn't it possible that the birds did increase call intensity, but were simply not willing (or able) to increase it to the same degree as the additional ambient noise?

This is an important question. The fact is that when ambient noise increases (at the relevant frequency channels), then the measured vocalizations will also increase. There is no way to separate the two effects. Thus, as scientists, when we cannot measure an effect, it is safer not to suggest an effect. Unfortunately, most studies that claim an increase in vocalizations' intensity in noise, do not account for this potential artifact (and most of them do not estimate noise at a species-specific level as we have done). This has created a lot of "noise" in the field. We do not want to criticize the Derryberry results without analyzing the data, but from reading their methods it does not seem like they took the noise into account in their acoustic measurements. But if you look at their figure 4A you will see a lot of variability in measuring the minimum frequency – which could be strongly affected by ambient noise.

In light of the above, we thus prefer to be careful and not to state changes that are probably false. We added some of this information to the manuscript. We also added the linear equations to the graph (in the caption of figure 3) where it can be seen that the slope is always ≤ 1 .

Reviewer 2:

The explanation of methods can be improved. For example, it is not clear if data were low-pass filtered before resampling to avoid aliasing.

We edited the methods and hopefully they are clearer now. Regarding the specific question – yes, an LPF was applied to prevent aliasing before the resampling. This information was added to the manuscript.

It is quite possible that birds move into the trees and further from the recorders with human activity. Since sound level decreases by the square of the distance of the source from the recorders, this could significantly affect the data. As indicated in the Discussion, this is a significant parameter that could not be controlled.

The reviewer is correct, and we addressed this point. Such biases could arise with any type of surveying including manual transects (except for perhaps, placing tags on the animals). We note that we only analyzed high SNR signals and that the species we selected somewhat overcome this bias – both crows and parakeets are not shy and Prinias are anyway shy and prefer to not be out in the open. We would also expect to see a stronger effect for human speech if this was a central phenomenon, and we did not see this, but of course this might have affected our results.

In interpreting the data, the authors mention the effect of human activity on bird vocalizations in the context of inter-species predator-prey interactions; however, the presence of humans could also modify intraspecies interactions by acting as triggers for communication of warning and alarm, and/or food calls (as may sometimes be the case) to conspecifics. Along the same lines, it is important to have a better understanding of the behavioral significance of the syllables used to monitor animal activity in the present study.

We agree with this point and added more discussion of both this potential bias and the type of syllables that were analyzed.

Another potential effect that may influence the results but is difficult to study, relates to the examination of vocalizations near to the ambient noise level. This is the bandwidth of sound levels where most significant changes may occur, for example, due to the Lombard effect demonstrated in bird and bat species. However, as indicated, these are also more difficult to track and quantify. Moreover, human generated noise, other than

speech, may be a more relevant factor in influencing acoustic activity of different bird species. Speech, per se, similar to the vocalizations of many other species, may simply enrich the acoustic environment so that the effects observed in the present study may be transient without significant long-term consequences.

We note that we already included a noise parameter (in addition to human speech) in the original manuscript. Following the reviewer's comment, we examined another factor, namely we replaced the previous ambient noise parameter with an estimate of ambient noise under 1kHz which should reflect most anthropogenic noise (not restricted to human speech). This model gave very similar results to the previous one (which is not very surprising as noise is usually correlated). We added this information to the revised manuscript, and we now also added examples of anthropogenic noise to the supplementary materials (Fig. S8). In general, we accept the comments made by the reviewer, but would like to emphasize that we only analyze high SNR vocalization (and not vocalizations that were close to the noise level). This strategy should have overcome biases that resulted from slight changes in ambient noise.

In general, the authors achieved their aim of illustrating the complexity of the effect of human activity on animal behavior. At the same time, their study also made it clear that estimating such effects is not simple given the dynamics of animal behavior. For example, seasonality, temperature changes, animal migration and movement, as well as interspecies interactions, such as related to predator-prey behavior, and inter/intra-species competition in other respects can all play into site-specific changes in the vocal activity of a particular species.

We completely agree and tried to further emphasize this in the revised manuscript. This is one of the main conclusions of this study – we should be careful when reaching conclusions.

Although the methods used in the present study are statistically rigorous, a multivariate approach and visualization techniques afforded by principal components analysis and multidimensional scaling methods may be more effective in communicating the overall results.

Following this comment, we ran a discriminant function analysis with the parameters of the best model (site category, ambient noise, human activity, temperature and lockdown state) with the task of classifying the level of bird activity. The DFA analysis managed to classify activity significantly above chance and the weights of the parameters revealed some insight about their relative importance. We added this information to the revised manuscript

Suggestions for improvement:

In Figure 2, the labeling of the Y-axis in the right panel should be moved to the left, similar to A and C. This will provide clear separation between the two side-to-side panels.

Revised

In Figure 3, it will be good to see the regression lines (as dashed lines) separately for the lockdown and no-lockdown conditions in addition to the overall effect.

Revised

Editor:

Limitations

Scale: The study's limited spatial and temporal scale was not addressed by the authors, which contrasts with the broader scope of other cited studies. To enhance the significance of the study, acknowledging and clearly highlighting this limitation, along with its potential caveats, modifications in the language used throughout the text would be beneficial. Furthermore, although the authors examined slight variations in habitat, it is important to note that all sites were primarily located within an urban landscape.

We revised the manuscript accordingly.

Control period: The control period is significantly shorter than the lockdown treatment period and occurs at a different time of year, potentially impacting the vocalization patterns of birds due to different annual cycle stages. It is crucial to consider that the control period falls within the pandemic timeframe despite being shortly after the lockdowns ended.

Revised – we included a control comparison to periods of equal length within the lockdown. People gradually stopped obeying the lockdown regulations before its removal so in fact, the official removal date is probably an overestimate for the effect of the lockdown. We now explain this.

Recommendations

Human-generated noise, beyond speech, might have a greater influence on the acoustic activity of various bird species, but previous studies lacked detailed human activity data. Instead of solely noting the number of human talkers, the authors could quantify other aspects of human activity such as vehicles or overall anthropogenic noise volume. Exploring the relationships between these factors and bird activity at a fine scale, while disentangling them from bird detection, would be compelling. It is important to consider the potential difficulty in resolving other anthropogenic sounds within a specific bandwidth, which could be demonstrated to readers through spectrograms and potential post-pandemic changes. Such information, including daily coefficient of variation/fluctuation rather than absolute frequency spectra, could provide valuable insights.

We note that we have already included an ambient noise factor (in addition to human speech) in the previous version. Following the reviewers' comments, we examined another factor, namely we replaced the current ambient noise parameter with the ambient noise under 1kHz which should reflect most of anthropogenic noise (not restricted to human speech). This model gave very similar results to the previous one (which is not surprising as noise is usually correlated). We also added several spectrograms in the Supplementary material that show examples of different types of noise.

Authors should limit their data interpretation to the impact of lockdown on behavioral responses within small-scale variations in habitat. A key critique is the assumption that activity changes solely resulted from the lockdown, disregarding other environmental factors and phenology.

Following the editor comment we realized that our conclusion/assertations were not clear. We never claimed that activity changes solely resulted from the lockdown. While revising the manuscript we ensured that we show a significant effect of temperature, ambient noise and human activity – all of which are not dependent on lockdown. We made an effort to emphasize the complexity of the system. We show that the lockdown seemed to have an additional impact, but we never claimed it was the only factor.

To address this, the authors could compare acoustic monitoring data within a shorter timeframe before and after the lockdown (20 days), while also controlling for temperature effects, to strengthen the validity of their claims. They would need to explain in their discussion, however, that such a comparison may still be confounded by any carry-over effects from the 10 days of treatment.

This analysis would be difficult because although the lockdown was officially removed at a specific date, it was gradually less respected by the citizens and thus the last period of the lockdown was somewhere between lockdown and no-lockdown. This is why we chose the approach of taking 10 days randomly from within the lockdown period and comparing them with the 10 post-lockdown days. We now clarify the reason better.

An option is that authors could frame their analysis as a study of the behavior of wildlife coming out of a lockdown, to draw a distinction from other studies that compared pre-pandemic data to pandemic data.

Good idea – revised.