Lockdown effects on fear: direct and indirect effects mediated by release of urban predators

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Abstract

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Lockdown effects on fear: direct and indirect effects mediated by release of urban predators

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Abstract: The Covid-19 lockdown reduced drastically human presence outdoors, providing an uncontrolled experiment for disentangling direct and indirect effects of human presence on animal fearfulness. We measured 18,494 flight initiation distances (FIDs, the distance at which individual animals fly away when approached by a human) from 1,333 populations of 202 bird species taken in four European cities both before, during and after the lockdown. Differential responses to lockdown among urban and rural habitats and between signing and non-singing birds showed that lockdown relaxed direct disturbance effects on birds in rural habitats, but increased indirect fear effects mediated by predator release (mainly feral cats) in cities.

Introduction

Animal fitness depends on a continuous balance between foraging, reproductive activities, and the associated risk of being depredated (Stephens & Krebs 1986). Human presence and activity produce direct and indirect effects on both sides of this balance. Wild predators are less abundant in human impacted habitats due to fear effects or to direct persecution (Díaz et al. 2013; Torre et al. 2022), whereas access to food and mates is usually higher for the individuals and species that best tolerate human presence (Ydenberg & Dill 1986). Heat island effect resulting in elevated temperatures in urban habitats, light pollution, or both, have additional positive effects on reproduction by extending the duration of reproductive periods in cities (Møller et al. 2015).

Behavior is a prime short-term response to changes in environmental conditions, which translate ecological effects into resource acquisition, interactions with hetero- and conspecifics, and use of resources for survival and reproduction (Huey et al. 2003). The so-called flight initiation distance (FID), the distance at which an animal flees when approached by a human observer under standardized conditions (Blumstein *2006)* , is a robust estimate of predator avoidance behavior, that involves a trade-off between avoidance of danger and acquisition of basic needs (Cooper & Blumstein 2015). FID increases under favorable climatic conditions that decrease caloric needs (Díaz et al. 2021) and with increasing abundance of natural and feral predators (Hediger 1934; St. Clair et al. 2010). Responses to human presence are however variable. FIDs are longer in urban than in nearby rural habitats, which implies negative relationships between human density and FID (Sol et al. 2013; Samia et al. 2015), but both positive and negative relationships within cities have been documented (Mikula 2014; Morelli et al. 2018; Carlen et al. 2021). Shorter FID in urban habitats is attributed to either habituation to human presence or to natural selection for fearless individuals under conditions of low predation risk (Samia et al. 2015; van Dongen et al. 2015; Johnson & Munshi-South 2017; Carrete et al. 2018), emphasizing the importance of direct effects of human disturbance on FIDs. However, indirect effects mediated by lower predation pressure in cities is also involved (Díaz et al. 2013; Samia et al. 2015). The 2020 lockdown established to control the Covid-19 pandemic was an excellent uncontrolled experiment for disentangling these direct and indirect effects (Rutz et al. 2020).

Flying animals have the opportunity to take advantage of 'escape in the third dimension' by adjusting fleeing behavior and post or perch height according to predation risk and display needs (Møller 2010). FIDs have in fact two components: the horizontal distance at which animals flee, and the height above ground at which they were located when flushed (Møller 2010). Different activities may modulate both predation risk and height selection. Singing birds tend to select higher posts to amplify sound transmission, exposing them more to aerial predators, which are more abundant in rural habitats, but less to ground predators, more abundant in cities (Møller 2011). Escape from the ground should be costlier than escape from higher perches (Hedenström & Alerstam 1992). Comparative analyses provided evidence for natural selection on song post height and adjustments in the vertical and horizontal components of escape behavior in relation to variation in predation risk associated with human presence. Birds having higher song posts and fleeing higher in the vegetation tend to have higher survival rates and lower senescence rates, a trend that is facilitated in urban habitats due to human effects on both aerial and ground-dwelling predators (Møller 2010).

Differential responses to lockdown are thus expected according to habitat, height above ground and singing behavior if indirect effects of humans on predators mediate effects of human presence on FIDs. These differences are not expected in a scenario of direct effects of human disturbance. Specifically, we expected a) shorter FIDs during lockdown than before and after, if responses to human presence were due to disturbance,

and longer FIDs if due to effects of indirect predator release effects (Díaz et al. 2013; Samia et al. 2015); b) lack of changes in height above ground in the former case, and increased height in the latter (Møller 2011; Díaz et al. 2022); c) differential lockdown effects in urban as compared to nearby rural habitats, with stronger changes in the latter (Díaz et al. 2021); d) differential changes for singing compared to non-singing birds, with weaker changes in the latter (Møller 2011); e) differential adjustments of vertical and horizontal components of FID, by increasing the latter according to the former (i.e. longer horizontal FIDs when individuals perch higher), according to lockdown, habitat and singing behavior (Møller 2010; Díaz et al. 2021); and f) delayed effects of lockdown on FIDs to the year after lockdown, as compared with pre-lockdown conditions, if fear responses to lockdown influenced individual fitness (Johnson & Munshi-South 2017).

Materials and Methods

Fieldwork was carried out in and around the cities of Brønderslev (Denmark), Paris (France), Madrid and Toledo (Spain; Supplementary file S1). We estimated flight initiation distance (FID, the distance at which individual birds flee when approached by a human under standardized conditions; Blumstein 2006) in paired urban and nearby rural sites located 1-20 km away (Díaz et al. 2013). Briefly, trained observers (APM in Denmark and France and MD in Spain) approached individual birds previously detected at least 20 m away by eye or with binoculars during random walks across study areas during the breeding seasons of 2018, 2020 and 2021. We recorded species, age, sex when possible, and whether the birds were singing or not when detected. We avoided sampling young birds or individuals engaged in nest building or offspring provisioning. Only one individual per species and sex was recorded at each specific site to avoid sampling the same individual more than once. We estimated horizontal distance at fleeing by pacing or by means of a Nikon Forestry 550 hypsometer. We estimated height above the ground when the bird was detected by eye or measured it with the hypsometer to the nearest 1 m. FIDs were calculated as the square root of the sum of the squared horizontal distance and the squared height above ground (Samia et al. 2015). Permission by the local authorities during the 2020 lockdown allowed sampling even at restricted sites (i.e. urban parks). We were thus able to sample during (2020) and after (2021) the Covid-19 lockdown in the same areas that we sampled before lockdown (2018) in previous studies (Díaz et al. 2013; 2021; 2022).

Effects of lockdown, habitat, singing behavior and their interactions on FIDs and their horizontal and vertical (perch or song post height) components were tested using generalized least square regression (PGLS) models on log10-transformed means for all individuals of the same species sampled in each habitat of each city (Díaz et al. 2013). We estimated the phylogenetic scaling parameter lambda (λ), that varies between 0 (phylogenetic independence) and 1 (complete phylogenetic trait conservatism or dependence (Freckleton et al. 2002), to calculate the phylogenetically corrected model estimates. We obtained a consensus phylogeny using Mesquite software (Maddison & Maddison 2011) on 100 trees extracted from the phylogeny published by Jetz et al. (2012; birdtree.org). Site effects were controlled for by including the different populations of the same species as polytomies with a constant small genetic distance of 0.0001 (Díaz et al. 2013) (Supplementary file S2). The inverse of sample sizes was used to correct for sampling effort (Garamszegi & Møller 2010). We used the R libraries ape, MASS and mvtnorm and the function pglm3.3.r (Supplementary file S3). We tested for adjustments between vertical and horizontal components of FID following the same modelling approaches, but using the log-transformed horizontal distance as the dependent variable, log-transformed height above ground as a covariate, and lockdown, habitat, singing behavior and their interactions with height as factors (Díaz et al. 2022). Effect sizes were computed as Pearson's product–moment correlation coefficients from t values (Lipsey & Wilson 2001) and were judged small ($r < 0.10$), intermediate ($r = 0.11$–0.49) or large ($r > 0.50$) following (Cohen 1988).

Results

We obtained 18,494 FID records from 1,333 populations of 202 bird species both before the Covid-19 lockdown (2018, N=3261 records, 319 populations), during lockdown (2020, N=3688 and 345) and after (2021, N=11,545 and 669; Appendix). Sample sizes were unbalanced because we used all FIDs taken from other studies on bird fear that we regularly conducted from 2006 onwards in the study sites (Díaz et al. 2013; 2021; 2022). Phylogenetic, site and sample size effects were significant in all models (Tables 1 and 2). Lock-

down, habitat and singing behavior had large effect sizes on FIDs and their components after controlling for these effects (Table 1). Lockdown also interacted with habitat and singing behavior with large effect sizes, although there were no three-way interactions (Table 1). FID and its horizontal component decreased during lockdown, then after it increased in rural habitats, especially for non-singing birds (Fig. 1). Singing birds, and non-singing birds in urban habitats, showed the same trend although less markedly so, and singing birds showed the opposite trend (increased FIDs during lockdown) in urban habitats. Mean post height of singing birds did not change in neither habitat and did not differ among habitats. Non-singing birds perched higher during lockdown, and higher in rural habitats; perch height remained higher before lockdown in urban habitats and decreased in rural habitats (Fig. 1).

Overall, birds did not horizontally adjust flight distance significantly according to the height above ground where they were located or perched. Rather, such adjustments were modulated by lockdown, habitat and singing behavior with moderate to large effect sizes. There were no significant higher-order interactive effects (Table 2). Horizontal distances were negatively related to height both before and after lockdown (i.e., birds that perched higher allowed for closer horizontal approaches), but this effect disappeared during lockdown (Fig. 2, above). Negative relationships between components were steeper in rural than in urban habitats, and birds allowed for closer approaches in urban habitats for the same perch height (Fig. 2, middle). Finally, non-singing birds modulated horizontal flight distances whereas singing birds did not (Fig. 3, below).

Discussion

Lockdown, habitat and singing behavior had clear-cut direct and interactive effects on FIDs and their horizontal and vertical components. Responses varied between urban and nearby rural habitats, and on whether birds were singing or engaged in other activities. Overall, direct disturbance effects seemed to predominate in rural habitats, where FIDs decreased by more than a half in non-singing birds to mean distances as short as in urban habitats. Weaker decreases were found for singing rural birds. Contrarily, no significant FID change was found for non-singing birds in urban habitats, whereas singing birds increased rather than decreased FIDs, as expected under increased risk of predation from ground-dwelling predators (Møller 2011). Mean height above ground of non-singing birds increased during lockdown in both urban and nearby rural habitats, also fitting expectations from increased risk of predation from ground-dwelling predators such as feral cats (Díaz et al. 2022). Singing birds posted higher than non-singing birds, and post height was not affected by either habitat or the lockdown, suggesting strong stabilizing selection for song post height selection and/or low behavioral flexibility for this trait (Møller 2011).

Birds that perched higher in the vegetation allowed for closer horizontal approaches than species perched lower (Møller 2010; but see Blumstein et al. 2004, Díaz et al. 2022*)* , a behavioral adjustment that tended to reduce the variability of FIDs towards a species- and site-specific mean value, and is associated to increased survival and reduced senescence (Møller 2011). Singing behavior and the Covid-19 lockdown suppressed this adjustment, implying higher FID variability during lockdown and more commonly singing birds. Adjustments were stronger in rural habitats, as expected by the lower variance in FID usually found in urban habitats, that has been interpreted as resulting from stabilizing selection of individuals able to endure high levels of human disturbance under conditions of low predation risk (Samia et al. 2015). Suppression of this adjustment during lockdown and in singing birds may have allowed individuals to better adjust horizontal and height components of FID to varying levels of predation risk coming from ground-dwelling predators released by human absence.

Overall, our results point to differential mechanisms underlying lockdown effects on bird fearfulness. Reduced direct disturbance seemed to predominate in rural habitats, where non-singing birds would have benefited from human absence. In urban habitats, however, human absence seemed to have increased the risk of predation by ground-dwelling predators, most likely the colonies of free-roaming feral cats maintained by animal-loving citizens (Díaz et al. 2022). Lockdown effects lagged to the following year, especially in urban habitats and for singing birds, suggesting stronger selection effects in sedentary urban and/or territorial populations than in more transient rural populations (Møller et al. 2013). Selection by these predators on bird scape behavior may explain time-lagged responses to lockdown in urban habitats, that may compensate

for effects of continued human presence on loss of antipredator behaviors (Geffroy et al. 2020).

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Supplementary Materials

Figure S1. Disease reveals the importance of urban predators. The Covid-19 lockout released bird fear in four European cities.

Table S1. Location and human population size of the study cities, and duration of lockdown in 2020 (taken from Wikipedia).

Table S2. Consensus phylogeny.

Table S3. R scripts.

Appendix. Mean, SE, minimum and maximum (m) Flight Initiation Distances and their horizontal and vertical components according to bird species, city, habitat (U: urban; R: rural surroundings), year (2018, Before the Covid-19 lockdown; 2020, During lockdown, and 2021, After it), and whether birds were singing or not when detected. N=sample size.

Fig 1. Mean Flight Initiation Distance (m +- SE) and its components before, during and after the 2020 lockdown associated with the Covid-19 pandemic. Filled symbols, lines: rural habitats; open symbols, dashed lines: urban habitats. Right: singing birds; left: non-singing birds

Fig 2. Adjustment of horizontal distances according to height above ground and their variation according to lockdown, habitat and singing behavior. Top graph (lockdown); grey dots, dashed line: After; filled dots, continuous lines: During; and open dots, pointed line: Before. Middle graph (habitat); filled squares, continuous line: rural; open squares, pointed line: urban. Bottom graph (singing behavior); filled diamonds continuous line: singing; open diamonds, pointed line: not singing). Note log10 (+1) transformations of both components. Lines are linear trends.

Table 1. Results of phylogenetically corrected analyses on the effects of lockdown, habitat, singing activity and their interactions on Flight Initiation Distances (FID) and their horizontal and vertical (height above ground) components. Model statistics, adjusted R2, AICc, the λ parameter measuring degree of phylogenetic dependence and its associated tests against the null hypothesis of independence, and the W parameter controlling for sample size effects, are also shown. Boldface indicates $p<0.05$. Effect sizes (r) were computed from F (F=[?]t) values following *(33)* .

Table 2. Results of phylogenetically corrected analyses on adjustments of the horizontal component of FID to the height above ground where the birds were posted or perched, and the effects of lockdown, habitat, singing activity and their interactions on these adjustments. Model statistics, adjusted R2, AICc, the λ parameter measuring degree of phylogenetic dependence and its associated tests against the null hypothesis of independence, and the W parameter controlling for sample size effects, are also shown. Boldface indicates $p<0.05$. Effect sizes (r) were computed from F (F=[?]t) values following *(33)* .

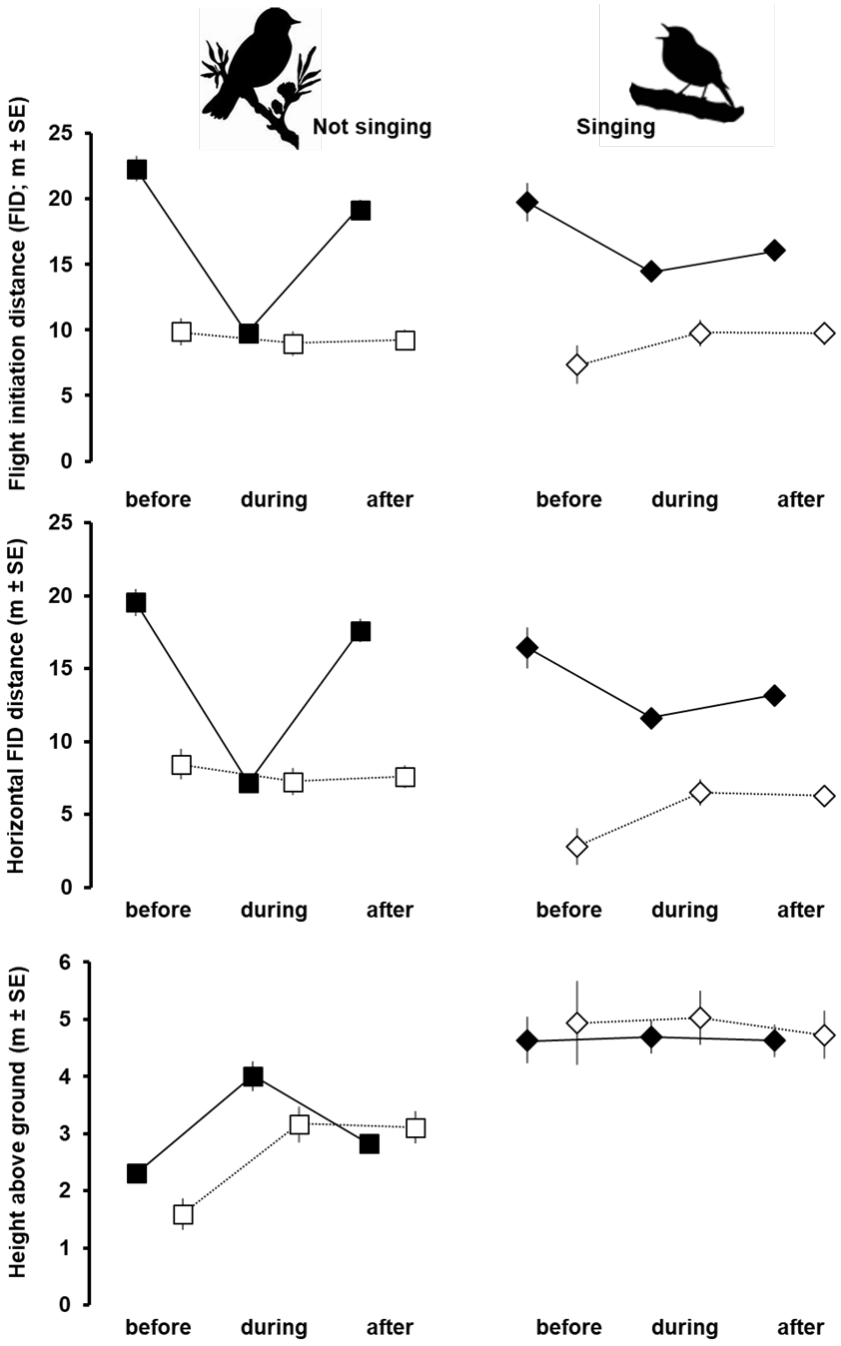

Fig. 1

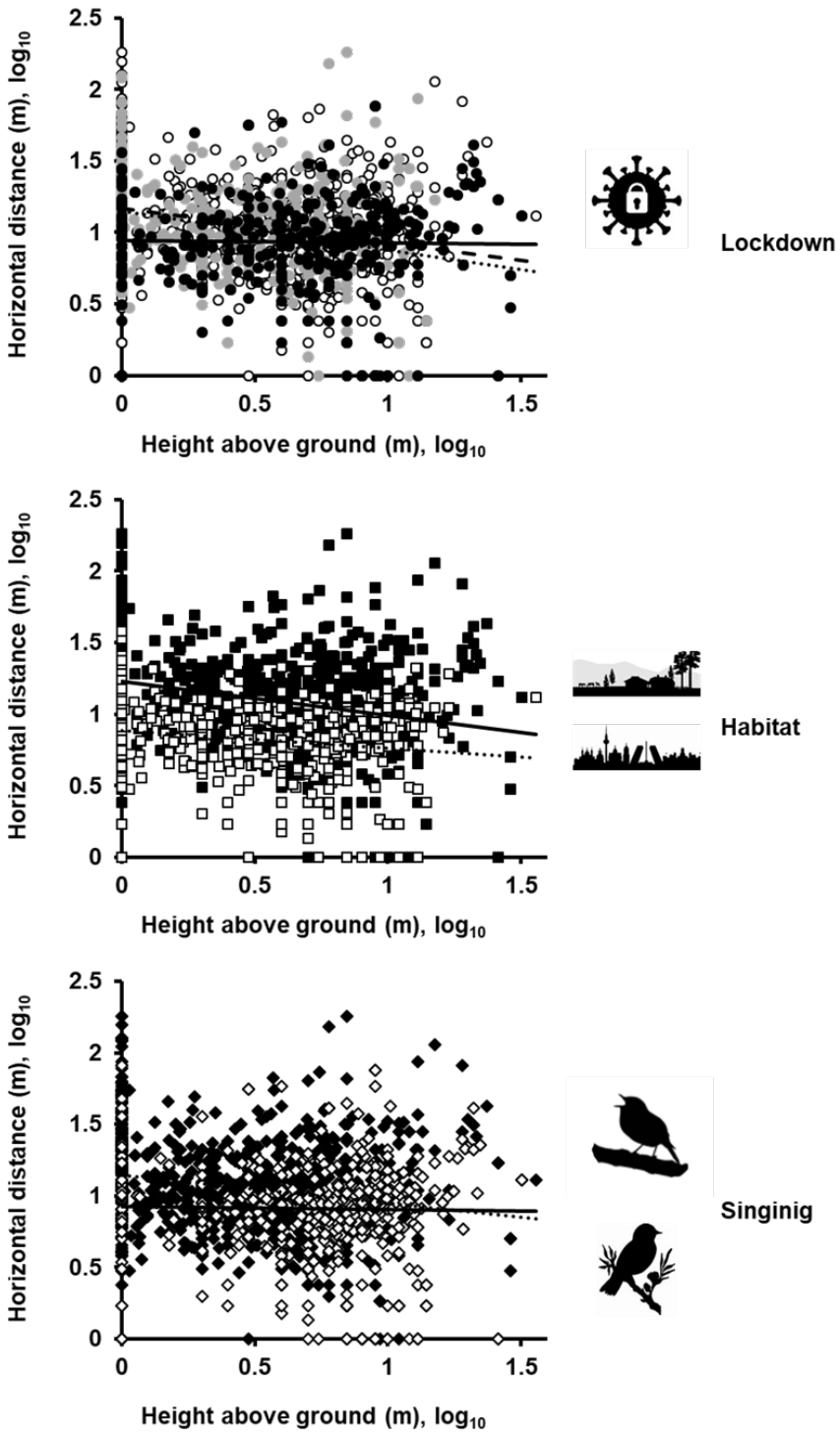

Fig. 2

Table 1 .

		FID	FID	FID	Horizontal distance
Source	df	F	p	effect size	F
Lockdown	2, 1132	4.53	**0.011**	**0.521**	6.59
Habitat	1, 1132	207.72	**0.000**	**1.000**	179.11
Singing	1, 1132	3.67	0.056	0.372	15.25
Lockdown x habitat	2, 1132	8.13	**0.000**	**0.891**	5.08
Lockdown x singing	2, 1132	9.18	**0.000**	**0.929**	9.23
Lockdown x habitat x singing	2, 1132	0.10	0.909	0.000	0.58
Model	12, 1144	23.96	**0.000**		21.76
Adjusted R^2		0.181			0.167
AICc		-329.56			251.54
Λ		0.759	χ^2_{12}= 314.91, p=0.000	χ^2_{12}= 314.91, p=0.000	0.546
W		100			300

Table 2 .

	Horizontal distance	Horizontal distance	Horizontal distance	Horizontal distance
Source	df	F	P	effect size
Log_{10}(height above ground)	1, 1126	3.15	0.076	0.284
Height x lockdown	2, 1126	4.26	**0.014**	**0.476**
Height x habitat	1, 1126	6.26	**0.012**	**0.760**
Height x singing	1, 1126	14.60	**0.000**	**0.988**
Height x lockdown x habitat	2, 1126	1.20	0.302	0.043
Height x lockdown x singing	2, 1126	2.13	0.120	0.134
Model	18, 1144	16.90	**0.000**	
Adjusted R^2		0.191		
AICc		255.93		
Λ		0.534	χ^2_{18}= 167.80, p=0.000	χ^2_{18}= 167.80, p=0.000
W		500		