Urban birds' flight responses were unaffected by the COVID-19 shutdowns

Peter Mikula[1*], Martin Bulla[2,3], Daniel T. Blumstein[4], Yanina Benedetti[2], Kristina Floigl[2], Jukka Jokimäki[5], Marja-Liisa Kaisanlahti-Jokimäki[5], Gábor Markó[6], Federico Morelli[2,7], Anders Pape Møller[8,9], Anastasiia Siretckaia[2], Sára Szakony[10], Michael A. Weston[11], Farah Abou Zeid[2], Piotr Tryjanowski[12†], Tomáš Albrecht[1,13†]

[1]Institute of Vertebrate Biology, Czech Academy of Sciences, Květná 8, 60365, Brno, Czech Republic

[2]Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 129, 165 00 Prague, Czech Republic

[3]Department of Behavioural Ecology and Evolutionary Genetics, Max Planck Institute for Ornithology, Eberhard Gwinner Str. 7, 82319 Seewiesen, Germany

[4]Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive, South, Los Angeles CA 90095–1606, USA

[5]Arctic Centre, University of Lapland, PO Box 122, 96101, Rovaniemi, Finland

[6]Department of Plant Pathology, Institute of Plant Protection, Hungarian University of Agriculture and Life Sciences, Ménesi út 44, 1118, Budapest, Hungary

[7]Institute of Biological Sciences, University of Zielona Góra, Prof. Z. Szafrana St. 1, 65-516, Zielona Góra, Poland

[8]Ecologie Systématique Evolution, Université Paris-Sud, CNRS, AgroParisTech, Université Paris-Saclay, F-91405, Orsay Cedex, France

[9]Ministry of Education Key Laboratory for Biodiversity Sciences and Ecological Engineering, College of Life Sciences, Beijing Normal University, 100875, Beijing, China

[10]Department of Ecology, Institute of Biology, University of Veterinary Medicine Budapest, Rottenbiller u. 50., H-1077, Budapest, Hungary

[11]School of Life and Environmental Sciences, Deakin University, Burwood Campus, 221 Burwood Highway, VIC 3125, Burwood, Australia

[12]Institute of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71C, 60-625, Poznań, Poland

[13]Department of Zoology, Faculty of Science, Charles University, Viničná 7, 12844, Prague, Czech Republic

*Author for the correspondence: petomikula158@gmail.com

†These authors jointly supervised this work

ORCID:

Peter Mikula: https://orcid.org/0000-0002-2731-9105

Martin Bulla: https://orcid.org/0000-0002-1328-1927

Yanina Benedetti: https://orcid.org/0000-0003-1600-2310

Daniel T. Blumstein: https://orcid.org/0000-0001-5793-9244

Jukka Jokimäki: https://orcid.org/0000-0002-7903-4128

Gábor Markó: https://orcid.org/0000-0003-1351-4070

Federico Morelli: https://orcid.org/0000-0003-1099-1357

Piotr Tryjanowski: https://orcid.org/0000-0002-8358-0797

Mike Weston: https://orcid.org/0000-0002-8717-0410

Tomáš Albrecht: https://orcid.org/0000-0002-9213-0034

Abstract

The coronavirus disease 2019 (COVID-19) pandemic has dramatically altered human activities, potentially relieving human pressures on urban-dwelling animals. Here, we evaluated whether birds from five cities in five countries (Czech Republic – Prague, Finland – Rovaniemi, Hungary – Budapest, Poland – Poznan, and Australia – Melbourne) changed their tolerance towards human presence (measured as flight initiation distance) during the COVID-19 shutdowns. We collected 6369 flight initiation distance estimates for 147 bird species and found that birds tolerated approaching humans to a similar level before and during the COVID-19 shutdowns. Moreover, during the shutdowns, bird escape behaviour did not consistently change with the level of governmental restrictions (measured as the stringency index). Hence, our results indicate that birds do not flexibly and quickly adjust their escape behaviour to the reduced human presence; in other words, the breeding populations of urban birds examined might already be tolerant of human activity and perceive humans as relatively harmless.

Keywords: antipredator behaviour; lockdown; escape distance; habituation; human-induced rapid environmental change; urbanisation

1. Introduction

The actions taken to control the coronavirus disease 2019 (hereafter COVID-19) pandemic have locked inhabitants in their dwellings and thus changed the pattern of human outdoor activities (Fang *et al.* 2020; Gatto *et al.* 2020; Huang *et al.* 2020; Kraemer *et al.* 2020; Randler *et al.* 2020; Venter *et al.* 2020a, b; March *et al.* 2021). This situation created a quasi-experiment that offers a unique opportunity to study how rapid changes in human behaviour affect wildlife (Derryberry *et al.* 2020; Manenti *et al.* 2020; Rutz *et al.* 2020; Zellmer *et al.* 2020; Soga *et al.* 2021; Soto *et al*. 2021). The shifts in human activity linked to the COVID-19 pandemic were tangible particularly in urban areas (Rutz *et al.* 2020; Park *et al.* 2021). Consequently, the COVID-19 shutdowns have elicited a complex mixture of positive and negative effects on urban nature (Bates *et al.* 2021), including changes in animal behaviour (Derryberry *et al.* 2020; Montgomery *et al.* 2021; Vardi *et al*. 2021).

The coexistence of wild animals with humans requires animals to tolerate human presence and consequent disturbance (Samia *et al.* 2015; Ducatez *et al.* 2020). Nevertheless, urban-dwelling animals are more tolerant of human approach than their rural conspecifics (Díaz *et al.* 2013; Samia *et al.* 2015, 2017; Mikula *et al.* 2021). Yet, how the intensity of human presence (e.g. human population or pedestrian density) precisely shapes the escape behaviour of urban animals is less clear. While some studies have revealed that tolerance to humans increased with increasing human presence at studied sites (Webb & Blumstein 2005; Mikula 2014), other studies reported much weaker, none or even opposite effects (Morelli *et al.* 2018; Gnanapragasam *et al.* 2021; Mikula *et al.* 2021). Whether the COVID-19 shutdowns induced changes in human activities which then altered the urban-landscape of fear is unknown.

The COVID-19 shutdowns locked people at homes and reduced their mobility within cities (Geng *et al*. 2021; Wu *et al*. 2021; but see Venter *et al*. 2020b) and thus created a natural experimental condition which could have affected the tolerance of urban animals towards humans (usually quantified as flight initiation or escape distance) in three ways. First, the lack of or reduced human presence during shutdowns might result in decreased animal tolerance to humans and consequently increased escape distances because (a) some studies have reported that animal tolerance decreases on the gradient from heavily human-visited (“disturbed”) sites to sites with low human activity (Webb & Blumstein 2005; Mikula 2014) and (b) escape distances of urban birds may also increase if less tolerant individuals and species colonise or at least increase their detectability in human-emptied landscapes (Manenti *et al.* 2020; Gordo *et al.* 2021). Second, due to reduced human activity, animal vigilance (i.e. the time spent monitoring for potential threats) might decrease, which in turn could increase animal tolerance to human presence because animal vigilance is often positively correlated with escape distance (Samia *et al.* 2013; Samia & Blumstein 2015), leading to reduced escape distances during the shutdowns (Montgomery *et al.* 2021). Third, animal responses to human disturbance may not change during the shutdowns if animals are already habituated to human activity and generally consider humans as harmless. Indeed, keeping escape distances constant may reduce unnecessary responses even when encounters are less frequent or reduction of already short escape distances may be constrained). In addition, if animals changed their escape distance during COVID-19 shutdowns, we expect that the change would follow the levels of governmental restrictions (stringency index) since the stringency index was negatively associated with human use of urban parks (Geng *et al*. 2020).

Here, we explored variation in avian tolerance towards humans before (breeding seasons before March 2020) and during the COVID-19 shutdowns (breeding seasons 2020–2021), and whether the tolerance to humans during the COVID-19 shutdowns changed according to the level of governmental restrictions. Avian tolerance towards human disturbance was measured as the flight initiation distance, the distance from an approaching human observer at which bird starts to escape (Albrecht & Klvaňa 2004; Stankowich & Blumstein 2005; Blumstein 2006; Weston *et al.* 2012; Díaz *et al.* 2013) and measured in four European cities (the Czech Republic – Prague; Finland – Rovaniemi; Hungary – Budapest; Poland – Poznan) and one in Australia (Melbourne).

2. Materials and Methods

2.1. Study areas

Flight initiation distances were collected in the Czech Republic (~90% of data collected by P.M.; the rest were collected by F.M., Y.B., K.F., A.S. and F.A.Z.), Finland (J.J. and field assistant), Hungary (G.M. and S.S.), Poland (P.T.), and Australia (M.W. and field assistants). All field data were collected during the breeding season (Europe: 1 April – 1 August; Australia: 15 August – 15 March) and only in urban areas, i.e. areas with continuous urban elements, including multi-story buildings, family houses, or roads, with built-up area >50%, building density >10/ha, residential human density >10/ha (Marzluff *et al.* 2001). Most data were collected in urban green areas, particularly parks and cemeteries. Czech data were collected in

Prague (50.083°N, 14.417°E; 1.3 million inhabitants, 177–399 m a. s. l.), Finnish in Rovaniemi (66.5°N, 25.733°E; 64,000 inhabitants, 75–203 m a. s. l.), Hungarian in Budapest (47.498°N, 19.041°E; 1.8 million inhabitants, 96–527 m a. s. l); Polish in Poznań (52.406°N, 16.925°E; 0.53 million inhabitants, 60–154 m a. s. l.); and Australian in Melbourne (37.821°S, 144.961°E; 5.2 million inhabitants, 5–169 m a. s. l.). For each city, we collected data for two breeding seasons before the pandemic, covering the 2018 and 2019 seasons immediately preceding the emergence of the COVID-19 (Finland, Hungary, Poland; and until March 2020 in Australia) and for up to two breeding seasons during the COVID-19 shutdowns (seasons starting in 2020 and 2021, for the Czech Republic, only starting in 2021). The 2019 data were not available for the Czech Republic, and thus we used 2014 and 2018. The flight initiation distances were collected during favourable weather conditions (i.e. no rain and no strong wind) mainly during the weekdays and during the early mornings (till 10:00).

2.2. Avian tolerance towards humans

Avian tolerance towards human approaches (“disturbance”) was estimated by a simple but widely used method, the flight initiation distance, i.e. the distance at which birds escape when approached by a human observer (Stankowich & Blumstein 2005; Blumstein 2006; Weston *et al.* 2012; Díaz *et al.* 2013). The flight initiation distance reflects a trade-off between the fitness-related benefits of not escaping and the costs of fleeing (Ydenberg & Dill 1986; Albrecht & Klvaňa 2004; Stankowich & Blumstein 2005; Samia *et al.* 2016). The flight initiation distance estimates are highly consistent for individuals, populations, and species tested within similar contexts (Carrete & Tella 2010; Díaz *et al.* 2013; Guay *et al.* 2016; Mikula *et al.* 2018).

All data were collected by trained researchers skilled in bird identification, and using a standard procedure outlined previously (Blumstein 2006; Samia *et al.* 2015; Mikula *et al.* 2018, 2021). Briefly, when a focal bird was spotted, a single observer moved at a normal walking speed (~1 ms^{-1}) directly towards the bird (with head and gaze oriented towards this bird). When the focal bird first started to escape (i.e. hopped, walked, ran, or flew away), the distance of the observer to the bird was noted. The escape distance was measured either by counting the number of ~1 m long steps, counting the number of steps of known approximate length and converting them to metres or using a rangefinder (with ±1 m resolution). The escape distance of birds positioned above the ground (e.g. perching on vegetation) was estimated as the Euclidean distance that equals the square-root of the sum of the squared horizontal distance and the squared height above the ground. We approached only individuals without initial signs of distress. Birds often occur in flocks; in these cases, we randomly selected a single individual from a flock and measured its response. All fieldworkers wore outdoor clothes without any bright colours. Within each city we collected data at many sites (at the level of park, cemetery, etc.); to avoid repeated sampling of the same individuals, we did not re-sample the same location during the same breeding season. Within the sampling occasion at a given site, the same species individuals were sampled only if it was obvious that they represent different individuals (e.g. because of their concurrent presence or if morphological features, e.g. sex-specific colouration or age, enabled us to distinguish between different individuals). In total, we collected 6369 flight initiation distance estimates for 147 bird species representing 2693 before-shutdowns estimates for 68 species and 3676 during-shutdowns estimates for 135 species.

2.3. Predictors and covariates

Each observation was scored as collected before (0) or during (1) the COVID-19 shutdowns (hereafter "Period").

To further explore whether changes in human activity during the shutdowns affected avian escape behaviour, we extracted data for each country and day on the strength of governmental measures characterised by governmental stringency index (hereafter "stringency index") from Our World in Data database (https://ourworldindata.org/covid-stringency-index, based on data originally published in Hale et al. (2021)). This index is rescaled to values from 0 to 100 (0 = no restrictions; 100 = strictest restrictions) and represents a composite measure based on nine response indicators, including school closures, workplace closures, cancellation of public events, restrictions on public gatherings, closures of public transport, stay-at-home requirements, public information campaigns, restrictions on internal movements, and international travel controls.

Life-history, social, contextual and environmental factors may influence escape responses of birds and potentially confound associations between avian escape responses and changes in human outdoor activity before and during the COVID-19 shutdowns. Hence, we extracted information on seven parameters. (1) The 'starting distance' (Blumstein 2006; Weston *et al.* 2012; Mikula *et al.* 2018) was estimated as the distance to the bird (in metres) when an observer started the escape distance trial. (2) The 'flock size' (Samia *et al.* 2015; Mikula *et al.* 2018;

Morelli *et al.* 2019) was calculated as the number of all conspecific individuals moving, feeding, or perching together that were visually separated from other conspecific or mixed-species individuals. Note that we avoided approaching mixed-species bird groups. (3) The species-specific ‘body size’ (Stankowich & Blumstein 2005; Díaz *et al.* 2013) was approximated as body mass (in grams) and obtained as the mean of female and male values from EltonTraits 1.0 database (Wilman et al. 2014). (4) The ambient ‘temperature’ (Reynolds *et al.* 2020) was estimated as the air temperature (°C) at the site during the data collection. (5) The ‘time’ of data collection (in hours) (Piratelli *et al.* 2015) was rounded to the nearest hour. (6) The date of data collection (Legagneux & Ducatez 2013; Piratelli *et al*. 2015; Mikula *et al*. 2018) was noted as a ‘day’ since the start of the breeding season (Europe: Day 1 = 1 April; Australia: Day 1 = 15 August). (7) The ‘site’ represents a unique identifier of each sampled park, cemetery, the city district, etc.

2.4. Statistical analyses

We used R version 4.3.0 (R Development Core Team 2021) for all statistical analyses. We used two sets of mixed effect models.

First, we explored the differences in escape behaviour of birds before and during the COVID-19 shutdowns by fitting the flight initiation distance (ln-transformed) as a response variable and a Period (0 – before, 1 – during shutdowns) as a predictor of interest, while controlling for starting distance (ln-transformed), flock size (ln-transformed), temperature (also a proxy for a day within the breeding season: $r_{\text{Pearson}} = 0.48$; Fig. S1) and time of day. To account for circular properties of time, time was transformed into radians ($2 \times \text{time} \times \pi/24$) and fitted as sine and cosine of radians (Bulla *et al.* 2016). All continuous variables were standardised by subtracting the mean and dividing by the standard deviation. Potential multicollinearity among explanatory variables was checked by the correlation matrix, which suggested that correlations between variables were generally weak (Fig. S1). To account for the non-independence of data points (Schielzeth & Forstmeier 2009; Barr *et al.* 2013), we attempted to fit random intercepts of year, genus, species, species at a given day and year, country, site, and species within a site, while fitting Period as random slope within all random intercept, except for year and species at given day and year. We then simplified the random structure of the model to avoid singular fit (Barr *et al.* 2013), i.e. a situation when one or more random effects are estimated as zero or close to zero. The outcomes of the models with alternative random structures were similar (Fig. S2;

Table S1). We used this approach with a full dataset with all observations (n = 6369), as well as with conservative datasets, one with at least five observations per species and Period (i.e. at least five observations before and five during the COVID-19 shutdowns; n = 5260), the other with at least 10 observations per species and each Period (n = 5106).

Second, we explored whether the escape behaviour of birds during the COVID-19 shutdowns was modulated by the varying levels of governmental restrictions, the stringency index. We thus used only data gathered during the shutdowns (i.e. Period = 1; n = 3676) and adopted the same models and the same random structure simplification procedure as for the first set of models on Period, but using stringency index instead of Period and year as fixed (not as random) effect. Similarly, as in the models for Period, varying the random structure did not influence the outcomes of the models, nor did limiting species to only those with at least five or at least 10 observations (Fig. S2; Table S2).

The models were fitted with the *lme4* package (Bates *et al*. 2015). We then used the sim function from the *arm* package and a non-informative prior distribution (Gelman & Hill 2007; Gelman & Su 2018) to create a sample of 5,000 simulated values for each model parameter (i.e. posterior distribution). We report effect sizes and model predictions by the medians, and the uncertainty of the estimates and predictions by the Bayesian 95% credible intervals represented by the 2.5 and 97.5 percentiles (95% CI) from the posterior distribution of 5,000 simulated or predicted values. We graphically inspected the goodness of fit, and the distribution of the residuals (see Bulla *et al*. 2022).

As the need for phylogenetic control depends on the phylogenetic signal in the residuals of the model (Uyeda *et al.* 2018), we tested whether the residual variance contained a phylogenetic signal. Thus, we extracted the residuals from the model on full data, presented in the main text (Fig. 1 – all data estimates; Period: Table S1 – model 1d, Stringency index: Table S2 – model 1c), and fitted the residuals as a new response variable in an intercept-only Bayesian linear regression fitted with STAN (Stan Development Team 2022) using *brm* function from *brms* package v. 2.17 (Bürkner 2017, 2018), with species and their phylogenetic relatedness as random effects. The phylogenetic relatedness was included as a phylogenetic covariance matrix calculated with inverseA function in the *MCMCglmm* v. 2.33 package (Hadfield 2010) from the maximum credibility tree build using maxCladeCred function in the *phangorn* v. 2.8.1 package (Schliep 2011) and 100 randomly sampled species-level phylogenetic trees (Hackett backbone) from BirdTree online tool (http://birdtree.org) (Jetz *et al.* 2012). Priors were specified using the *get_prior* function from *brms*, which uses Student's t distribution for the intercept and standard deviation (Bürkner 2017). The target average proposal acceptance probability was increased to 0.99 to make the sampling more conservative to posterior distributions with high curvature (Bürkner 2017). Five MCMC chains ran for 5,000 iterations each while discarding the first 2,500 iterations as burn-in, and sampling every 5th iteration, which resulted in 5,000 samples of model parameters. The independence of samples in the Markov chain was assessed using graphic diagnostics and the convergence using the Gelman-Rubin diagnostics which was 1 for all parameters, indicating model convergence (Brooks & Gelman 1998). Phylogeny explained zero (for Period model, 95%CI: 0–0.2% of variance in random effects) or little variation (3.6% [0–16%] for a Stringency index model) and the models without phylogeny fitted the data on residuals better than the models with phylogeny (i.e. the estimated Bayes factor in favour of non-phylogenetic model was 155 for Period and 100 for Stringency index, their posterior probabilities 0.995 and 0.986 respectively), which justifies our use of non-phylogenetic comparative methods.

All results are reproducible with the open-access data and code available from Bulla *et al*. (2022), which also provides visual representations of model assumptions.

3. Results

We found no consistent differences in avian tolerance towards humans (i.e. in their escape distance) before and during the COVID-19 shutdowns (Figs 1a, 2, S2–S4; Table S1). Moreover, during the shutdowns, we found no clear changes in escape distance in relation to the strength of governmental COVID-19 restriction, i.e. stringency index, (Figs 1b and 3; Table S2). These results were robust to changes in random effects structure and sample size (Fig. S2; Tables S1 and S2). The within and between species responses highly varied and changed within and between species, as well as within and between sites and years (Figs 2 and 3, Figs S3 and S4).

4. Discussion

Our observations of avian tolerance towards humans (measured as escape distance) revealed that populations of urban birds did not exhibit major shifts in their tolerance towards humans (a) between periods before and during the COVID-19 shutdowns and (b) as a function of the stringency of governmental COVID-19 restrictions. Responses to both the shutdowns and the stringency of governmental restrictions varied widely across spatial and temporal scales. Altogether, our results indicate that escape responses of sampled breeding populations of urban birds are unaffected by temporal changes in human presence and abundance at studied sites. This is consistent with some degree of urban tolerance not being further modified by even dramatic changes in human activity patterns and could reflect the (1) differential settlement of bold and shy individuals in and outside cities, (2) natural selection on urban tolerance, or (3) habituation-like processes reducing plasticity.

First, the escape distance of birds is an individual trait, i.e. flight initiation distance is highly consistent within individuals tested under similar contexts (Carrete & Tella 2010; Díaz *et al.* 2013; Guay *et al.* 2016; Mikula *et al.* 2018). If the urban environment filters birds based on inherent levels of tolerance towards human disturbance with bold and shy individuals inhabiting areas with varying levels of human disturbance (Carrete & Tella 2010, 2013; van Dongen *et al*. 2015), the lack of consistent change in escape behaviour of urban birds during the COVID-19 shutdowns may indicate an absence or generally low influx of shy, less tolerant individuals and species from rural areas into studied cities. Although some studies have reported animal species that occupied new areas changed their local abundance, or shifted the timing of their main activity in response to change in human activities during the COVID-19 pandemic, these changes are often area- or species-specific and did not occur everywhere (Manenti *et al.* 2020; Bates *et al.* 2021; Gordo *et al.* 2021; Vardi *et al.* 2021). Importantly, it remains to be shown whether such “changes” in animal behaviour are real or an artefact of increased activity of researchers and citizen scientists in cities during the COVID-19 pandemic (Basile *et al.* 2021; Crimmins *et al.* 2021; Hochachka *et al.* 2021; Randler *et al*. 2021).

Second, another possibility is that the lack of change in avian tolerance towards humans is a result of an adaptation to urban lifestyle, i.e. evolutionary change in escape response due to natural selection on urban tolerance (Symonds *et al.* 2016). Species entering urban environments have larger brains (Sayol *et al*. 2020), greater innovation and problem-solving abilities (Audet *et al*. 2016; Ducatez *et al*. 2017; Griffin *et al*. 2017), are less neophilic and habituate to novel conditions faster than rural birds (Tryjanowski *et al.* 2016; Vincze *et al.* 2016; Griffin *et al.* 2017). Indeed, birds that colonised urbanised areas earlier are more tolerant toward humans (Symonds *et al*. 2016). Yet, it is possible that avian tolerance reaches limits (e.g. in an extreme case, not escaping would translate to being stepped upon) after several generations living in cities. Indeed, escape responses persist in even the most habituated birds. Our results may thus indicate that natural selection on escape behaviour of these species living in the cities is currently at an optimum; hence, the changes in human presence associated with COVID-19 shutdowns were insufficient and too temporary to select for different escape distances.

Third, our results may indicate that the examined breeding populations of birds were already habituated to or otherwise tolerant of human presence and abundance and humans might have been generally perceived as harmless, irrespective of the number of people outside (Ellenberg *et al.* 2009; Rankin *et al.* 2009; Zaccaroni *et al.* 2010). Previous studies have found that changes in human density and activity may strongly influence escape behaviour of animals, especially when working with dichotomic comparison of natural (rural) and human-inhabited (urban) areas (Díaz *et al.* 2013). For example, neotropical birds occurring close to small and recently established human settlements, such as farms, have dramatically shorter escape distances (i.e. higher tolerance towards humans) than their counterparts living further from these settlements (Tryjanowski *et al.* 2020). However, studies exploring associations between escape behaviour of animals and various human activity regimes within urban areas revealed mixed results, indicating that within urban areas association between escape behaviour of animals and human density is often absent or weak (Morelli *et al.* 2018; Mikula *et al.* 2021). Such a finding, along with ours, contradict the expectation that "...we expect location-specific habituation where even a slight deviation in a predator's (or human's) routine behaviour can re-elicit fearful responses" (Samia *et al.* 2015). Our results indicate a minor role of behavioural plasticity in observed patterns and may indicate that habituation-like processes have already reduced plasticity.

Finally, worldwide, quarantine and stay-at-home orders have reduced the use of public spaces, particularly in cities. Yet, the changes in the use of public spaces during COVID-19 shutdowns seem to be country specific and dependent on the type of the public space (Derryberry *et al.* 2020; Randler *et al.* 2020; Rutz *et al.* 2020; Venter *et al.* 2020b; Geng *et al.* 2021). For example, the restrictions on social gathering and movement, as well as the closures of workplaces and indoor recreational facilities were associated with increased visits to parks in Norway (Venter *et al.* 2020b). However, on a global scale stay-at-home restriction and the stringency of governmental restrictions was negatively correlated with park visitation (Geng *et al.* 2020). Thus, the lack of a general change in escape distances of birds during COVID-19 shutdowns in our sample might be due to heterogeneous effects of country-specific governmental measures on human densities across cities and their outdoor space. We note that country explained up to 15% in escape distance during the COVID-19 shutdowns (Table S2), country and site explained little variance in the escape distance before and during the COVID-19 shutdowns (Table S1), escape distance changed stochastically across years and species (Fig. S4) and country-specific effects were largely absent in our data (Figs 2 and 3) suggesting inconsistent effects even within the countries (cities). Importantly, the changes in use of urban green-spaces during the COVID-19 shutdowns should be similar within a specific city. Thus, even if the use of public green spaces increased in some of our studied cities and decreased in others, we should, but do not, see consistent city-specific escape distance responses of the studied species (Figs 2, 3, S3 and S4). In other words, despite dramatic changes in human outdoor presence the studied populations of birds did not adjust their tolerance to humans again supports the idea that the urban bird populations are already habituated to human presence and resilient to fluctuations in human densities and encounters. The results of our study might also help to explain why several previous studies haven't detected increased probability of occurrence of wildlife in emptied cities (e.g. Gordo *et al.*, 2021; Vardi et al., 2021) – even lower than casual human activity in cities may require sharp behavioural adjustments in wild-living animals.

In conclusion, human population, and hence disturbance, is predicted to further increase during the 21st century (Sanderson *et al.* 2002). Therefore, animals will be increasingly forced to occupy human-altered environments, and altered environments will host more humans. Our results indicate that urban birds do not flexibly and quickly modify their escape behaviour to a temporarily reduced human presence, rather the birds had similar levels of tolerance towards humans in pre- and during-pandemic periods, and regardless of the stringency of governmental measures. In other words, our results reveal a degree of urban tolerance that is not further modified by even dramatic changes in human activity patterns. Whether such tolerance reflects a differential settlement of individuals in cities, natural selection on urban tolerance, or habituation-like processes that reduce plasticity requires detailed investigation. Studies of individually-marked birds that are repeatedly tested over time (*sensu* Carrete & Tella 2010, 2013), will be particularly important as will unambiguous quantification of individual birds' history of exposure to humans. There is an important role of experimental manipulations of human densities in the studied areas and on capitalising on large changes in population size over short periods of time which might be associated with natural disasters as well as rapid urban development. These observations of animal behaviour under various regimes of human activity and disturbance can help us quantify costs and benefits of behavioural responses to humans. Such insights help us better understand how species tolerate humans and, importantly, how urbanisation modifies behaviour.

Acknowledgments

M.W. thanks Eliza Anderson, Mickey Balzereit, Sammi Cunningham, Alisha Dabonde, Chloe Daws, Megan Dennis, Zoe Kellett, Clement Masse, Aaron Moore, Bailey Raats, Max Radvan, Frost Rebecca, Anthony Rendall, Natalie Searle, Mel Sheedy, Will Standish, Mia Stott, and Millie Toomey for help with the collection of escape responses of birds in Melbourne. Clement Masse helped us with data collection in Rovaniemi. J.J. was partly supported by the project "Responsible Tourism Planning" (2019-2023; project number 326348) founded by the Academy of Finland (PROFI 5 Competitive funding to strengthen universities' research profiles).

Ethical approval

The fieldwork protocols comply with the current laws of the countries. This kind of research requires no special permits in Europe. In Australia, Animal ethics approvals (Deakin University Animal Ethics Committee Permits B10-2018 and B08-2021) and permits (DEWLP, 10008731 and 10010123) were obtained. All fieldwork was conducted in accordance with the approved guidelines. Data were collected in public places and on private lands where no special permit was required. The method used to estimate avian tolerance towards human disturbance was designed to cause only brief and minimal disturbance to birds; in cities, this disturbance typically does not differ from standard background disturbance caused by other site visitors.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data statement

Data and computer code used to generate the results, as well as all supporting material including the plots of model assumptions are freely available from Open Science Framework repository https://doi.org/10.17605/OSF.IO/WUZH7 (Bulla *et al*. 2022).

References

Albrecht, T. & Klvaňa, P. (2004). Nest crypsis, reproductive value of a clutch and escape decisions in incubating female mallards *Anas platyrhynchos*. *Ethology*, 110, 603–613.

Audet, J.-N., Ducatez, S. & Lefebvre, L. (2016). The town bird and the country bird: problem solving and immunocompetence vary with urbanization. *Behavioral Ecology*, 27, 637–644.

Barr, D.J., Levy, R., Scheepers, C. & Tily, H.J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, 68, 255–278.

Basile, M., Russo, L.F., Russo, V.G., Senese, A. & Bernardo, N. (2021). Birds seen and not seen during the COVID-19 pandemic: The impact of lockdown measures on citizen science bird observations. *Biological Conservation*, 256, 109079.

Bates, A.E., Primack, R.B., Biggar, B.S., Bird, T.J., Clinton, M.E., Command, R.J., *et al.* (2021). Global COVID-19 lockdown highlights humans as both threats and custodians of the environment. *Biological Conservation*, 263, 109175.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.

Blumstein, D.T. (2006). Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Animal Behaviour*, 71, 389–399.

Brooks, S.P. & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, 7, 434–455.

Bulla, M., Blumstein, D.T., Benedetti, Y., Floigl, K., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., Markó, G., Morelli, F., Siretckaia, A., Szakony, S., Weston, M.A., Zeid, F.A., Tryjanowski, P., Albrecht, T. & Mikula, P. (2022). Supporting information for 'Urban birds' flight responses were unaffected by the COVID-19 shutdowns'. *Open Science Framework* https://doi.org/10.17605/OSF.IO/WUZH7.

Bulla, M., Valcu, M., Dokter, A.M., Dondua, A.A., Kosztolányi, A., Rutten, A., *et al.* (2016). Unexpected diversity in socially synchronized rhythms of shorebirds. *Nature*, 540, 109–113.

Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80, 1–28.

Bürkner, P.-C. (2018). Advanced Bayesian multilevel modeling with the R package brms. *The R Journal*, 10, 395–411.

Carrete, M. & Tella, J.L. (2010). Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance- induced habitat selection. *Biology Letters*, 23, 167–170.

Carrete, M. & Tella, J.L. (2013). High individual consistency in fear of humans throughout the adult lifespan of rural and urban burrowing owls. *Scientific Reports*, 3, 1–7.

Crimmins, T.M., Posthumus, E., Schaffer, S. & Prudic, K.L. (2021). COVID-19 impacts on participation in large scale biodiversity-themed community science projects in the United States. *Biological Conservation*, 256, 109017.

Derryberry, E.P., Phillips, J.N., Derryberry, G.E., Blum, M.J. & Luther, D. (2020). Singing in a silent spring: Birds respond to a half-century soundscape reversion during the COVID-19 shutdown. *Science (1979)*, 370, 575–579.

Díaz, M., Møller, A.P., Flensted-Jensen, E., Grim, T., Ibáñez-Álamo, J.D., Jokimäki, J., *et al.* (2013). The geography of fear: a latitudinal gradient in anti-predator escape distances of birds across Europe. *PLoS ONE*, 8, e64634.

Ducatez, S., Audet, J. N., Rodriguez, J. R., Kayello, L. & Lefebvre, L. (2017). Innovativeness and the effects of urbanization on risk-taking behaviors in wild Barbados birds. *Animal Cognition*, 20, 33–42.

Ducatez, S., Sol, D., Sayol, F. & Lefebvre, L. (2020). Behavioural plasticity is associated with reduced extinction risk in birds. *Nature Ecology & Evolution*, 1–6.

Ellenberg, U., Mattern, T. & Seddon, P.J. (2009). Habituation potential of yellow-eyed penguins depends on sex, character and previous experience with humans. *Animal Behaviour*, 77, 289–296.

Fang, H., Wang, L. & Yang, Y. (2020). Human mobility restrictions and the spread of the Novel Coronavirus (2019-nCoV) in China. *Journal of Public Economics*, 191, 104272.

Gatto, M., Bertuzzo, E., Mari, L., Miccoli, S., Carraro, L., Casagrandi, R., *et al.* (2020). Spread and dynamics of the COVID-19 epidemic in Italy: Effects of emergency containment measures. *Proc Natl Acad Sci U S A*, 117, 10484–10491.

Gelman, A. & Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, Cambridge.

Gelman, A. & Su, Y.-S. (2018). *arm: Data analysis using regression and multilevel/hierarchical models*. Available at: http://CRAN.R-project.org/package=arm. Last accessed 18 May 2022.

Gelman, A., Su, Y.-S., Yajima, M., Hill, J., Pittau, M., Kerman, J., *et al.* (2016). Data Analysis Using Regression and Multilevel/Hierarchical Models. *CRAN Repository*.

Geng, D.C., Innes, J., Wu, W. & Wang, G. (2021). Impacts of COVID-19 pandemic on urban park visitation: a global analysis. *Journal of Forestry Research*, 32, 553-567.

Gnanapragasam, J.J., Ekanayake, K.B., Ranawana, K., Symonds, M.R.E. & Weston, M. (2021). Civil war is associated with longer escape distances among Sri Lankan birds. *The American Naturalist*, 198, 653-659.

Gordo, O., Brotons, L., Herrando, S. & Gargallo, G. (2021). Rapid behavioural response of urban birds to COVID-19 lockdown. *Proceedings of the Royal Society B: Biological Sciences*, 288, 20202513.

Griffin, A. S., Netto, K. & Peneaux, C. (2017). Neophilia, innovation and learning in an urbanized world: a critical evaluation of mixed findings. *Current Opinion in Behavioral Sciences*, 16, 15–22.

Guay, P.J., van Dongen, W.F.D., Robinson, R.W., Blumstein, D.T. & Weston, M.A. (2016). AvianBuffer: An interactive tool for characterising and managing wildlife fear responses. *Ambio*, 45, 841–851.

Hadfield, J.D. (2010). MCMC methods for multi-response generalised linear mixed models: the MCMCglmm R package. *Journal of Statistical Software*, 33, 1–22.

Hadfield, J.D. & Nakagawa, S. (2010). General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology*, 23, 494–508.

Hale, T., Angrist, N., Goldszmidt, R., Kira, B., Petherick, A., Phillips, T., *et al.* (2021). A global panel database of pandemic policies (Oxford COVID-19 Government Response Tracker). *Nature Human Behaviour 2021 5:4*, 5, 529–538.

Hochachka, W.M., Alonso, H., Gutiérrez-Expósito, C., Miller, E. & Johnston, A. (2021). Regional variation in the impacts of the COVID-19 pandemic on the quantity and quality of data collected by the project eBird. *Biological Conservation*, 254, 108974.

Huang, X., Li, Z., Jiang, Y., Li, X. & Porter, D. (2020). Twitter reveals human mobility dynamics during the COVID-19 pandemic. *PLOS ONE*, 15, e0241957.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012). The global diversity of birds in space and time. *Nature*, 491, 444–448.

Kraemer, M.U.G., Yang, C.H., Gutierrez, B., Wu, C.H., Klein, B., Pigott, D.M., *et al.* (2020). The effect of human mobility and control measures on the COVID-19 epidemic in China. *Science (1979)*, 368, 493–497.

Legagneux, P. & Ducatez, S. (2013). European birds adjust their flight initiation distance to road speed limits. *Biology Letters*, 9, 20130417.

Manenti, R., Mori, E., di Canio, V., Mercurio, S., Picone, M., Caffi, M., *et al.* (2020). The good, the bad and the ugly of COVID-19 lockdown effects on wildlife conservation: Insights from the first European locked down country. *Biological Conservation*, 249, 108728.

March, D., Metcalfe, K., Tintoré, J. & Godley, B.J. (2021). Tracking the global reduction of marine traffic during the COVID-19 pandemic. *Nature Communications 2021 12:1*, 12, 1–12.

Marzluff, J.M., Bowman, R. & Donnelly, R. (2001). A historical perspective on urban bird research: trend, terms, and approaches. In: *Avian Ecology and Conservation in an Urbanizing World* (eds. Marzluff, J.M., Bowman, R. & Donnelly, R.). Kluwer, New York, pp. 20–47.

Mikula, P. (2014). Pedestrian density influences flight distances of urban birds. *Ardea*, 102, 53–60.

Mikula, P., Díaz, M., Albrecht, T., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., Kroitero, G., *et al.* (2018). Adjusting risk-taking to the annual cycle of long-distance migratory birds. *Scientific Reports*, 8, 13989.

Mikula, P., Jokimäki, J., Kaisanlahti-Jokimäki, M.L., Markó, G., Morelli, F., Møller, A.P., *et al.* (2021). Face mask-wear did not affect large-scale patterns in escape and alertness of urban and rural birds during the COVID-19 pandemic. *Science of The Total Environment*, 793, 148672.

Montgomery, R.A., Raupp, J. & Parkhurst, M. (2021). Animal Behavioral Responses to the COVID-19 Quietus. *Trends in Ecology & Evolution*, 36, 184–186.

Morelli, F., Benedetti, Y., Díaz, M., Grim, T., Ibáñez-Álamo, J.D., Jokimäki, J., *et al.* (2019). Contagious fear: Escape behavior increases with flock size in European gregarious birds. *Ecology and Evolution*, 9, 6096–6104.

Morelli, F., Mikula, P., Benedetti, Y., Bussière, R., Jerzak, L. & Tryjanowski, P. (2018). Escape behaviour of birds in urban parks and cemeteries across Europe: Evidence of behavioural adaptation to human activity. *Science of the Total Environment*, 631–632, 803–810.

Park, M., Lim, J.T., Wang, L., Cook, A.R. & Dickens, B.L. (2021). Urban-Rural Disparities for COVID-19: Evidence from 10 Countries and Areas in the Western Pacific. *Health Data Science*, 2021, 1–9.

Piratelli, A.J., Favoretto, G.R. & de Almeida Maximiano, M.F. (2015). Factors affecting escape distance in birds. *Zoologia (Curitiba)*, 32, 438–444.

R Development Core Team. (2021). *A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Randler, C., Tryjanowski, P., Jokimäki, J., Kaisanlahti-Jokimäki, M. L., & Staller, N. (2020). SARS-CoV2 (COVID-19) Pandemic lockdown influences nature-based recreational activity: The case of birders. *International journal of environmental research and public health*, 17, 7310.

Rankin, C.H., Abrams, T., Barry, R.J., Bhatnagar, S., Clayton, D.F., Colombo, J., *et al.* (2009). Habituation revisited: An updated and revised description of the behavioral characteristics of habituation. *Neurobiology of Learning and Memory*, 92, 135–138.

Rutz, C., Loretto, M.C., Bates, A.E., Davidson, S.C., Duarte, C.M., Jetz, W., *et al.* (2020). COVID-19 lockdown allows researchers to quantify the effects of human activity on wildlife. *Nature Ecology and Evolution*, 4, 1156–1159.

Samia, D.S.M. & Blumstein, D.T. (2015). Birds Flush Early and Avoid the Rush: An Interspecific Study. *PLOS ONE*, 10, e0119906.

Samia, D.S.M., Blumstein, D.T., Díaz, M., Grim, T., Ibáñez-Álamo, J.D., Jokimäki, J., *et al.* (2017). Rural-urban differences in escape behavior of european birds across a latitudinal gradient. *Frontiers in Ecology and Evolution*, 5, 66.

Samia, D.S.M., Blumstein, D.T., Stankowich, T. & Cooper, W.E. (2016). Fifty years of chasing lizards: new insights advance optimal escape theory. *Biological Reviews*, 91, 349–366.

Samia, D.S.M., Nakagawa, S., Nomura, F., Rangel, T.F. & Blumstein, D.T. (2015). Increased tolerance to humans among disturbed wildlife. *Nature Communications*, 6, 8877.

Samia, D.S.M., Nomura, F. & Blumstein, D.T. (2013). Do animals generally flush early and avoid the rush? A meta-analysis. *Biology Letters*, 9, 20130016.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A. v. & Woolmer, G. (2002). The Human Footprint and the Last of the Wild: The human footprint is a global map of human influence on the land surface, which suggests that human beings are stewards of nature, whether we like it or not. *BioScience*, 52, 891–904.

Sayol, F., Sol, D. & Pigot, A.L. (2020). Brain size and life history interact to predict urban tolerance in birds. *Frontiers in Ecology and Evolution*, 8, 58.

Schielzeth, H. & Forstmeier, W. (2009). Conclusions beyond support: overconfident estimates in mixed models. *Behavioral Ecology*, 20, 416–420.

Schliep, K.P. (2011). phangorn: phylogenetic analysis in R. *Bioinformatics*, 27, 592–593.

Soga, M., Evans, M.J., Cox, D.T.C. & Gaston, K.J. (2021). Impacts of the COVID-19 pandemic on human–nature interactions: Pathways, evidence and implications. *People and Nature*, 3, 518–527.

Sol, D., Lapiedra, O. & González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Animal Behaviour*, 85, 1101–1112.

Sol, D., Maspons, J., Gonzalez-Voyer, A., Morales-Castilla, I., Garamszegi, L.Z. & Møller, A.P. (2018). Risk-taking behavior, urbanization and the pace of life in birds. *Behavioral Ecology and Sociobiology*, 72, 59.

Sol, D., Timmermans, S. & Lefebvre, L. (2002). Behavioural flexibility and invasion success in birds. *Animal Behaviour*, 63, 495–502.

Soto, E.H., Botero, C.M., Milanés, C.B., Rodríguez-Santiago, A., Palacios-Moreno, M., Díaz-Ferguson, E., Velázquez, Y.R., Abbehusen, A., Guerra-Castro, E., Simoes, N., Muciño-Reyes, M. (2021). How does the beach ecosystem change without tourists during COVID-19 lockdown? *Biological Conservation*, 255, 108972.

Stan Development Team (2022). RStan: the R interface to Stan. R package version 2.21.5. Available at https://mc-stan.org/.

Stankowich, T. & Blumstein, D.T. (2005). Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society of London B: Biological Sciences*, 272, 2627–2634.

Symonds, M. R., Weston, M. A., Van Dongen, W. F., Lill, A., Robinson, R. W. & Guay, P. J. (2016). Time since urbanization but not encephalisation is associated with increased tolerance of human proximity in birds. *Frontiers in Ecology and Evolution*, 4, 117.

Tryjanowski, P., Kosicki, J.Z., Hromada, M. & Mikula, P. (2020). The emergence of tolerance of human disturbance in Neotropical birds. *Journal of Tropical Ecology*, 36, 1–5.

Tryjanowski, P., Møller, A. P., Morelli, F., Biaduń, W., Brauze, T., Ciach, M., Czechowski, P., Czyz, S., Dulisz, B., Golawski, A., Hetmański, T., Indykiewicz, P., Mitrus, C., Myczko, L., Nowakowski, J.J., Polakowski, M., Takacs, V., Wysocki, D. & Zduniak, P. (2016). Urbanization affects neophilia and risk-taking at bird-feeders. *Scientific Reports*, 6, 1–7.

Uyeda, J.C., Zenil-Ferguson, R. & Pennell, M.W. (2018). Rethinking phylogenetic comparative methods. *Systematic Biology*, 67, 1091–1109.

van Dongen, W. F., Robinson, R. W., Weston, M. A., Mulder, R. A. & Guay, P. J. (2015). Variation at the DRD4 locus is associated with wariness and local site selection in urban black swans. *BMC Evolutionary Biology*, 15, 1–11.

Vardi, R., Berger-Tal, O. & Roll, U. (2021). iNaturalist insights illuminate COVID-19 effects on large mammals in urban centers. *Biological Conservation*, 254, 108953.

Venter, Z.S., Aunan, K., Chowdhury, S. & Lelieveld, J. (2020a). COVID-19 lockdowns cause global air pollution declines. *Proc Natl Acad Sci U S A*, 117, 18984–18990.

Venter, Z.S., Barton, D.N., Gundersen, V., Figari, H. & Nowell, M. (2020b). Urban nature in a time of crisis: Recreational use of green space increases during the COVID-19 outbreak in Oslo, Norway. *Environmental Research Letters*, 15, 104075.

Webb, N. v & Blumstein, D.T. (2005). Variation in Human Disturbance Differentially Affects Predation Risk Assessment in Western Gulls. *Condor*, 107, 178–181.

Weston, M.A., McLeod, E.M., Blumstein, D.T. & Guay, P.-J. (2012). A review of flight-initiation distances and their application to managing disturbance to Australian birds. *Emu*, 112, 269–286.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world’s birds and mammals. *Ecology*, 95, 2027–2027.

Wu, C., Guo, Y., Guo, H., Yuan, J., Ru, L., Chen, H., Du, B. & Zhang, L. (2021). An investigation of traffic density changes inside Wuhan during the COVID-19 epidemic with GF-2 time-series images. *International Journal of Applied Earth Observation and Geoinformation*, 103, 102503.

Ydenberg, R.C. & Dill, L.M. (1986). The economics of fleeing from predators. *Advances in the Study of Behavior*, 16, 229–249.

Zaccaroni, M., Ciuffreda, M., Paganin, M. & Beani, L. (2010). Does an early aversive experience to humans modify antipredator behaviour in adult Rock partridges? *http://dx.doi.org/10.1080/08927014.2007.9522561*, 19, 193–200.

Zellmer, A.J., Wood, E.M., Surasinghe, T., Putman, B.J., Pauly, G.B., Magle, S.B., *et al.* (2020). What can we learn from wildlife sightings during the COVID-19 global shutdown? *Ecosphere*, 11, e03215.

Figure 1. Changes in avian tolerance towards humans (measured as the flight initiation distance) (a) before vs during the COVID-19 shutdowns and (b) due to stringency of governmental restrictions during COVID-19 shutdowns. The dots with horizontal lines represent estimated standardised effect size and their 95% confidence intervals based on the joint posterior distribution of 5000 simulated values generated by the *sim* function from the *arm* package (Gelman *et al.* 2016) using the mixed model outputs (Tables S1 and S2). The colour highlights the investigated association with Period before vs during the COVID-19 shutdowns – (blue) and stringency index (green). Depicted are effect sizes based on full and reduced datasets with ≥5 or ≥10 observations per species and period. Note that all estimates centre around zero.

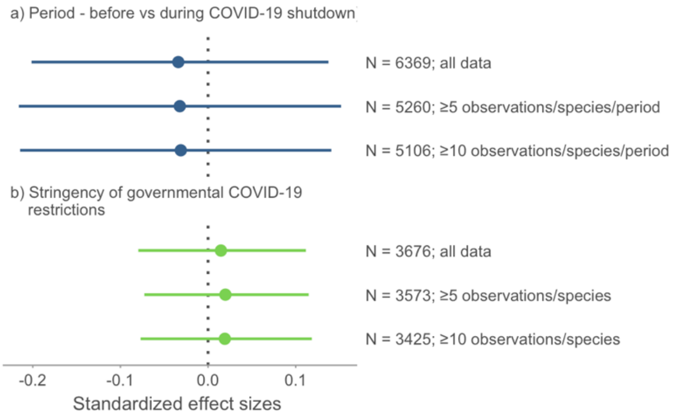


Figure 2. Avian tolerance towards humans (measured as the flight initiation distance) before and during the COVID-19 shutdowns according to genus. Dots represent means or single escape distance observations of species at specific sites (e.g. specific park or cemetery) with data for both periods (before and during the shutdowns) and not corrected for other factors such as starting distance of the observer. Dot colour highlights the country (Australia in violet, the Czech Republic blue, Finland turquoise, Hungary green, and Poland yellow). Dotted lines indicate no difference, dots above the line indicate lower tolerance towards humans (i.e. longer escape distances), dots below the line indicate lower tolerance before than during the COVID-19 shutdowns. Panels are ordered according to evolutionary history of birds with top left panels representing the oldest genera, and bottom right, the youngest. Panel titled 'other' contains genera with only one or two data points. The axes are on the log-scale. Note the within- and between-genera and cross-country variation and stochasticity in response to the shutdowns (for species-specific plots see Fig. S3, for within- and between-year variation Fig. S4) and that using escape distance values controlled for starting distance had little influence on the depicted relationships (Fig. S5). Silhouette of *Garrulus glandarius*, *Motacilla alba*, *Picus viridis*, *Phoenicurus ochruros*, *Sylvia borin* were drawn by Martin Bulla and are available at https://doi.org/10.17605/OSF.IO/WUZH7 (Bulla *et al*. 2022), silhouette of *Erithacus rubecula* drawn by Rebecca Groom, and silhouettes of *Fringilla coelebs* and *Sturnus vulgaris* by Maxime Dahirel and available at PhyloPic (http://phylopic.org); all these silhouettes are under Creative Commons Attribution 3.0 Unported licence (https://creativecommons.org/licenses/by/3.0/). The remaining silhouettes are available at PhyloPic under the Public Domain Dedication 1.0 license (https://creativecommons.org/publicdomain/zero/1.0/).

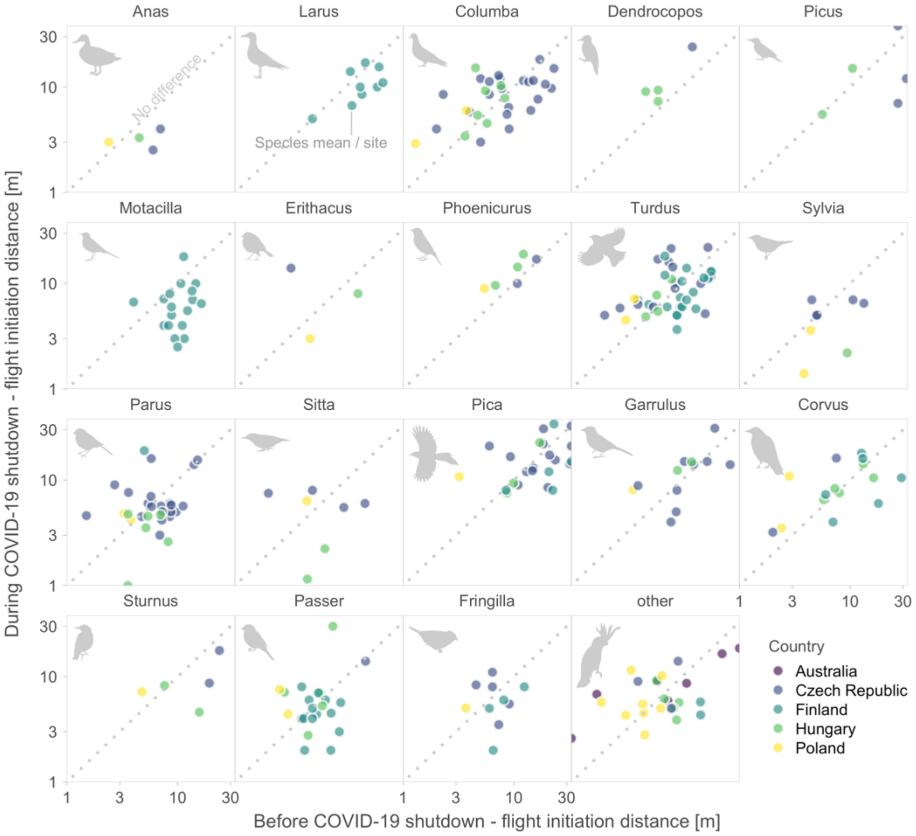
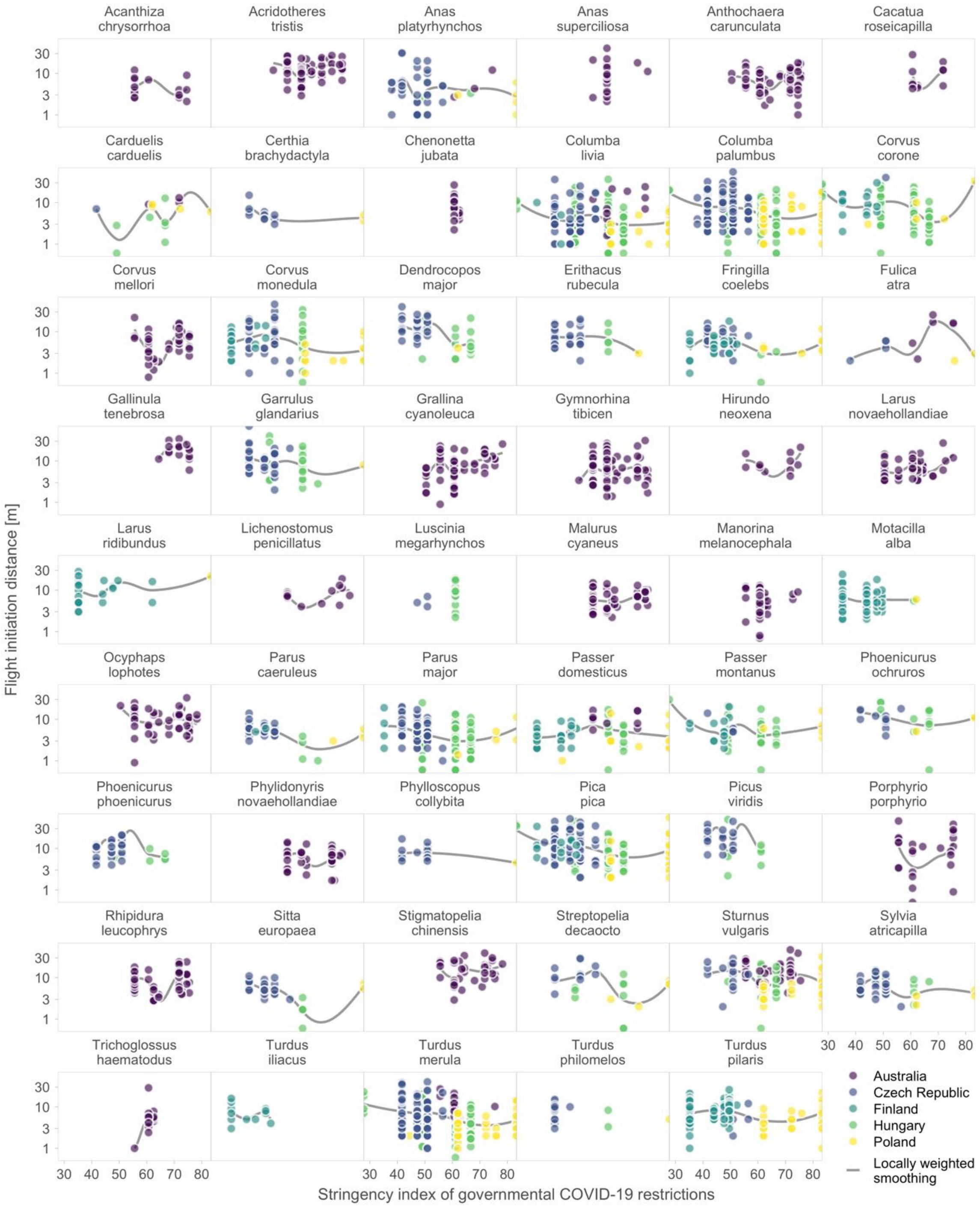

Anas
Larus
Columba
Dendrocopos
Picus
Motacilla
Erithacus
Phoenicurus
Turdus
Sylvia
Parus
Sitta
Pica
Garrulus
Corvus
Sturnus
Passer
Fringilla
other
No difference
Species mean / site
30
10
3
1
1
3
10
30
During COVID-19 shutdown - flight initiation distance [m]
Before COVID-19 shutdown - flight initiation distance [m]
Country
● Australia
● Czech Republic
● Finland
● Hungary
● Poland

Figure 3. Species-specific avian tolerance towards humans (measured as the flight initiation distance) in relation to severeness of governmental restrictions during COVID-19 shutdowns quantified as a stringency index. Each dot represents a single escape distance observation (not corrected for other factors such as starting distance of the observer) and a day-specific value of governmental stringency index in a given country. Dot colour highlights the country (Australia in violet, the Czech Republic blue, Finland turquoise, Hungary green and Poland yellow). Grey lines represent locally weighted smoothing, a non-parametric local regression fitted with the *ggplot* function of *ggplot2* package (Wickham 2016), highlighting heterogenous (and usually unclear) within- and between- species trends. Note, the y-axes is on the log-scale, some species lack trend lines because data distribution hindered the smoothing and visualised are only data for species with ≥10 escape distance observations.


Acanthiza chrysorrhoa
Acridotheres tristis
Anas platyrhynchos
Anas superciliosa
Anthochaera carunculata
Cacatua roseicapilla
Carduelis carduelis
Certhia brachydactyla
Chenonetta jubata
Columba livia
Columba palumbus
Corvus corone
Corvus mellori
Corvus monedula
Dendrocopos major
Erithacus rubecula
Fringilla coelebs
Fulica atra
Gallinula tenebrosa
Garrulus glandarius
Grallina cyanoleuca
Gymnorhina tibicen
Hirundo neoxena
Larus novaehollandiae
Larus ridibundus
Lichenostomus penicillatus
Luscinia megarhynchos
Malurus cyaneus
Manorina melanocephala
Motacilla alba
Ocyphaps lophotes
Parus caeruleus
Parus major
Passer domesticus
Passer montanus
Phoenicurus ochruros
Phoenicurus phoenicurus
Phylidonyris novaehollandiae
Phylloscopus collybita
Pica pica
Picus viridis
Porphyrio porphyrio
Rhipidura leucophrys
Sitta europaea
Stigmatopelia chinensis
Streptopelia decaocto
Sturnus vulgaris
Sylvia atricapilla
Trichoglossus haematodus
Turdus iliacus
Turdus merula
Turdus philomelos
Turdus pilaris
Flight initiation distance [m]
30
10
3
1
30 40 50 60 70 80
Stringency index of governmental COVID-19 restrictions
Australia
Czech Republic
Finland
Hungary
Poland
Locally weighted smoothing