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Habitat selection of three gull species in response to sudden changes in human mobility

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Developing robust strategies for human–wildlife coexistence is hampered by our limited understanding of how humans impact animal space use. It is challenging to measure the relative effects of landscape modification and human mobility on wildlife, since these factors are typically confounded. The extreme change in human mobility levels that occurred during COVID-19 lockdowns provided an opportunity to disentangle these impacts. Many gull species are considered urban adapters, capable of roosting, foraging and breeding near humans in highly modified environments. We predicted that lockdown-induced changes in human mobility would affect gulls' selection for urban and beach habitats because of altered disturbance levels and food availability. We analysed GPS tracking data from 113 individual gulls over multiple years (2015–2022), across three species in western Europe (herring gull *Larus argentatus*, lesser black-backed gull *L. fuscus* and yellow-legged gull *L. michahellis*). We found that, during lockdowns, selection for urban areas increased in two of ten colonies and selection for beaches increased in one colony and decreased in two others. This heterogeneous pattern likely reflects differences in how gull populations respond to opportunities and challenges presented by human-modified landscapes. Understanding this context dependence is emerging as a priority for coordinated efforts to promote sustainable human–wildlife coexistence.

1. Introduction

Humans are profoundly altering the Earth system, with devastating impact on the natural world [1]. Understanding how animals respond to human activity is crucial if we are to slow rates of biodiversity loss [2], by mitigating the effects of urban expansion and land transformation [3]. Many animals respond to anthropogenic pressures by altering their movement patterns [4,5], which can affect their survival and reproduction, and ultimately, the viability of populations [6]. Wildlife is probably sensitive to both the static (land modification: habitat fragmentation, buildings, roads and infrastructure) and dynamic (human mobility: the movement of humans and their vehicles, and any by-products) components of human activity, but measuring their relative impacts is challenging, since they are typically confounded. In 2020, lockdowns imposed during the COVID-19 pandemic caused sudden, large-scale changes in human mobility levels, providing an opportunity—under tragic circumstances—to disentangle these effects [7–11].

As COVID-19 lockdowns reduced pedestrian, road, air and marine traffic [11,12], many animal species appeared to change their behaviour [8]. Terrestrial mammals started moving into urban areas and approaching roads more closely [13–15], while many bird species altered their habitat use [11,16–18]—although responses varied markedly across species and sites [8,13,19]. In an age of major anthropogenic impacts, it is critical to understand why some species appear to cope well in areas of high human activity, while others do not, so that we can develop context-appropriate environmental planning and conservation management strategies that effectively promote human–wildlife coexistence.

Many gull species are considered successful urban adapters, capable of roosting, foraging and breeding near humans in highly modified environments [20,21]. As generalists, they routinely take advantage of urban and agricultural landscapes and fisheries activities [22–26]. They also exploit food sources in urban areas, even modifying their foraging behaviour to synchronize with human activity rhythms and track the availability of anthropogenic resources [27–30]. Gulls' behavioural plasticity and close association with humans make them an interesting group for investigating wildlife responses to pandemic lockdowns.

We analysed GPS tracking data from 113 individual gulls, from three species in western Europe, to investigate whether habitat selection changed in response to lockdowns. Unlike other studies examining animal movement behaviour during the pandemic (e.g. [15]), we were able to compare the peak lockdown year (2020) not just to one, but several baseline years, both before and after lockdown (2015–2019, 2021–2022), allowing assessment of inter-annual variability in habitat selection. We predicted that gulls' selection for urban and beach habitats would change in response to notable shifts in human mobility observed during lockdown [31] (electronic supplementary material, table S21) because of altered levels of disturbance and food availability. To interpret potential responses, we used our knowledge of relevant local context—both in terms of lockdown impacts and gull behaviour [32,33].

2. Material and methods

(a) Data collation

The COVID-19 Bio-Logging Initiative was launched in 2020 as a community-led research consortium under the umbrella of the International Bio-Logging Society [10]. A global call for collaboration was shared with members of the Society, other relevant networks and on social media. This was followed by targeted engagement of gull research groups known to us or identified through searching relevant publications and the Movebank data repository. Data providers joined the initiative by accepting its terms of collaboration.

In total, nine gull datasets (see electronic supplementary material, table S1) were suitable for use in collaborative analyses, with 113 individuals from ten colonies of three species (herring gull *Larus argentatus*, lesser black-backed gull *L. fuscus* and yellow-legged gull *L. michahellis*) included in final analyses. Using the STRANGE framework for animal behaviour research [34], we identified the following potential sampling biases: sex (see electronic supplementary material, table S2), age and breeding

status; and varying numbers of tagged individuals available across colonies and species. These biases need to be considered when attempting to generalize our study's findings to the source populations, and beyond.

(b) Data processing

We included in our analyses adult gulls that had been tracked in 2020 and at least one other year in 2015–2022. We chose not to include juvenile individuals because we expected that their habitat selection (and other behaviours) could have changed between years simply as a result of maturation, rather than in response to environmental changes caused by lockdowns. We also excluded data from five colonies with fewer than five tracked individuals (three of these had only two birds), which we deemed insufficient for estimating colony-level effects and because we allowed the random intercept variance to vary by colony (i.e. a minimum sample of five is typically recommended to achieve robust estimates of variance [35]); this left a minimum number of seven tracked individuals per colony and a total of 353 bird-years. We removed GPS locations that were estimated from fewer than four satellites, as well as outliers based on a ground speed threshold of 100 km h⁻¹ [36]. In the *amt* package [37] in R [38], we used the 'time_of_day' function to identify daytime and night-time periods and then remove night-time fixes.

(c) Habitat selection analyses

We used integrated step selection analysis (iSSA) to measure the habitat selection of gulls [39]. Briefly, iSSA parametrizes a biased correlated random walk for each individual, consisting of a movement process and habitat selection (for a review, see [40]). GPS locations are converted into 'steps', which are the displacement between consecutive locations sampled at a constant time interval (here, 30 minutes). Each integrated step selection function (iSSF) is fit by pairing each observed step with a set of available steps used for numerical integration [41], making it possible to estimate the parameters via conditional logistic regression. Available steps are sampled with random draws from 'tentative' parametric step length and turn angle distributions; here, we chose a gamma distribution to model step lengths and a von Mises distribution to model turn angles. Terms are included in the model to update the tentative distributions (here, step length, log of step length and cosine of turn angle), thereby estimating the movement process jointly with habitat selection. The fitted habitat selection parameters can be interpreted as log relative selection strengths (log-RSS) [42].

We included data from June and July (i.e. when individuals were likely to be resident on their breeding range) for habitat selection analyses, ensuring that the analysis period matched across years for each individual, to reduce biases in between-year comparisons. We removed data of five individuals (2 years for one of these) because inspection of GPS tracks revealed that they had not been resident during the analysis period.

We used the 'track_resample' function from the *amt* package to identify bursts of constant step duration, with rate = 30 minutes and tolerance = 4 minutes. We then used the 'steps_by_burst' function to create steps between fixes in bursts that had a consistent sampling rate. For each track (i.e. per individual per year), we used the 'random_steps' function in the *amt* package to generate 30 random steps for each observed step (for rationale, see above; [43]). Next, we annotated the end points of each step with Coordination of Information on the Environment (CORINE) program land cover classification data [44]. The CORINE land cover dataset has a resolution of 100 m and comprises 44 land cover types, which are grouped into two higher levels of classification (with 15 and 5 levels, respectively). We used three land cover types: urban (urban fabric; industrial, commercial and transport units; mine, dump and construction sites; and artificial, non-agricultural vegetated areas), beaches and 'other' (all remaining land cover classes pooled) (see electronic supplementary material, table S3). We also produced the centroid (median longitude and latitude) for each GPS track and then calculated the distance to centre for all points because most gulls were expected to exhibit central-place foraging behaviour during the analysis period. We only included tracks (i.e. bird-years) that had a minimum of 200 observed steps.

We fit separate iSSFs for each bird-year of data, using the *amt* function 'fit_issf'. We included land cover type ('other' set as the intercept) and *distance to centre* (scaled) as predictor variables, with *step length*, *log step length* and the *cosine of the turning angle* included as movement parameters; *step_id* identified the strata (i.e. the groupings of actual steps with their associated random steps). For each iSSF, we calculated the log-RSS for each land cover type compared to the 'other' reference land cover category. To calculate log-RSS values and standard errors, we used the *amt* function 'log_rss', with *distance to centre* = 0 m (note that this variable is centred, so 0 m equates to the mean distance to centre for each individual), *step length* = 100 m, *log step length* = 100 m and *cosine of the turning angle* = 1. We then aggregated the log-RSS values for all individuals and years for further statistical analysis. In this case, RSS for a particular land cover type is interpreted as how many times more likely a gull would be to choose that category over the 'other' reference level, given an equal choice between the two; note that we present our results on the log scale (i.e. log-RSS).

(d) Statistical analyses

We used the *brms* R package [45] to fit Bayesian mixed-effects models to test whether the log-RSS values were different in 2020 (lockdown) compared to non-lockdown years (note that we include 2021 in the non-lockdown group because restrictions were largely lifted during the June–July analysis period). We ran separate models for each species and land cover type (i.e. urban and beaches). The two land cover types were not always present in the fitted iSSFs because not all tagged gulls had each land cover type available in their home ranges, so sample sizes of aggregated log-RSS values vary between the land cover types.

Each model included fixed effects for *lockdown* and *colony* and their interaction. We included a random intercept for individual ID, with group-level variance allowed to vary by colony to account for heterogeneous individual-level variation across colonies, and we assumed that errors were normally distributed. All models were weighted by the inverse variance (mean normalized) of the log-RSS values, giving less influence to log-RSS estimates with lower precision (e.g. [46–48]). We assigned weakly informative priors to the fixed effects, specifying normal distributions with mean 0 and standard deviation 1000. For each model, we ran four parallel Markov chain Monte Carlo chains of 4000 iterations and discarded the first 1000 iterations as burn-in, resulting in 12 000 iterations for inference. All model parameters had Gelman-Rubin convergence diagnostic statistics (R) below 1.1, and effective sample sizes exceeded 1000. We visually inspected trace plots to confirm adequate chain mixing and convergence. Model fit was further evaluated by examining posterior predictive distributions. We considered effects to be statistically supported where 95% credible intervals (CIs) did not cross zero. We used the expert knowledge of each colony's respective field team to contextualize and interpret any changes in habitat selection observed in 2020.

Because all birds were of breeding age and gulls are known to exhibit high breeding site fidelity [49], we expected that any difference in habitat selection during 2020, compared to the non-lockdown baseline, would be related to behaviours such as foraging, loafing and roosting. However, to investigate whether our results were sensitive to potential biases associated with inter-annual differences in gull breeding behaviour, we refit the models including *breeding status* as a fixed effect with two categories (breeding or non-breeding) based on the identification of potential nest locations (see electronic supplementary material). Finally, even though most pandemic restrictions were lifted in our study areas during June and July 2021, we refit models excluding data from 2021, to investigate the robustness of our findings (see electronic supplementary material). Note that after excluding data from 2021, the yellow-legged gull colony at San Pedro had insufficient data, with just three individuals, to include in this sensitivity analysis for both the urban and beach habitat selection models.

3. Results

Among the three gull species investigated (figure 1*a–b*), herring gulls were most associated with urban land cover ($n = 21$ individuals; 48% [range: 2–91%] of used locations were classed as urban land cover in non-lockdown years compared to 51% [5–89%] during 2020), followed by lesser black-backed gulls ($n = 85$; 21% [0.1–81%] and 23% [0.1–70%]) and yellow-legged gulls ($n = 7$; 8% [3–16%] and 5% [2–10%]) (figure 1*b*).

Log-RSS for urban land cover increased during lockdown compared to non-lockdown years for one herring gull colony in Belgium (colony = Oostende: change in log-RSS = 0.66 [95% CI = 0.29, 1.04], $n = 7$ individuals) and for one lesser black-backed gull colony in the Netherlands (Neeltje Jans: change in log-RSS = 0.49 [0.16, 0.82], $n = 12$ individuals; but see sensitivity analysis below), with no change observed for the remaining eight colonies (electronic supplementary material, table S4; figure 2).

Log-RSS for beach land cover increased during lockdown compared to non-lockdown years for one lesser black-backed gull colony in England (Havergate: change in log-RSS = 1.07 [0.34, 1.81], $n = 11$ individuals), decreased for one lesser black-backed gull colony in the Netherlands (Schiermonnikoog: change in log-RSS = -0.62 [-1.14, -0.11], $n = 9$ individuals) and one yellow-legged gull colony in Spain (San Pedro: change in log-RSS = -1.38 [-2.34, -0.40], $n = 7$ individuals) and showed no significant change for the remaining four colonies that had beaches nearby (electronic supplementary material, table S4; figure 3).

All results were similar when the *breeding* term was included, except we found support for an increase in log-RSS for beach land cover during lockdown compared to non-lockdown years in one additional herring gull colony (Neeltje Jans: change in log-RSS = 0.29 [0.008, 0.56], $n = 11$ individuals; see electronic supplementary material, table S5, S7–S20). Likewise, all results were similar when excluding data from 2021, except the change in urban land cover selection for the lesser black-backed gull colony in the Netherlands was no longer supported (Neeltje Jans: change in log-RSS = 0.20 [-0.26, 0.65], $n = 8$ individuals) (see electronic supplementary material, tables S6, S7–S20).

4. Discussion

(a) Main findings

We found: (i) that selection for urban land cover increased in one population of herring gulls and one population of lesser black-backed gulls during COVID-19 lockdown, but not in the remaining eight colonies; (ii) that one colony of lesser black-backed gulls showed an increased preference for beach land cover, while one colony of lesser black-backed gulls and one colony of yellow-legged gulls exhibited a decrease; and (iii) that most of our tagged birds appeared unaffected by lockdowns (although they may have responded in other ways not captured by our methodology; see below). This mixed pattern of responses provides a valuable opportunity to explore—leveraging site-specific knowledge of environmental conditions and gull behaviour—how gulls are impacted by human disturbance and to what degree they rely on anthropogenic food resources.

Overall, the dietary flexibility of gulls likely explains why selection for urban habitat was similar in lockdown and non-lockdown years for most of the colonies investigated. Gulls from peri-urban colonies have greater trophic niche size than those from non-urban colonies, suggesting that urban environments provide a wide range of foraging resources [50], potentially allowing gulls to respond to fluctuations in the relative availability of different dietary components—such as anthropogenic waste from bins, kiosks and restaurants; food provided for birds; birds and rodents; earthworms and arthropods in parks; and fish and crabs in urban waterways [23,51–55]. Gulls may have responded to changes in human mobility by using different

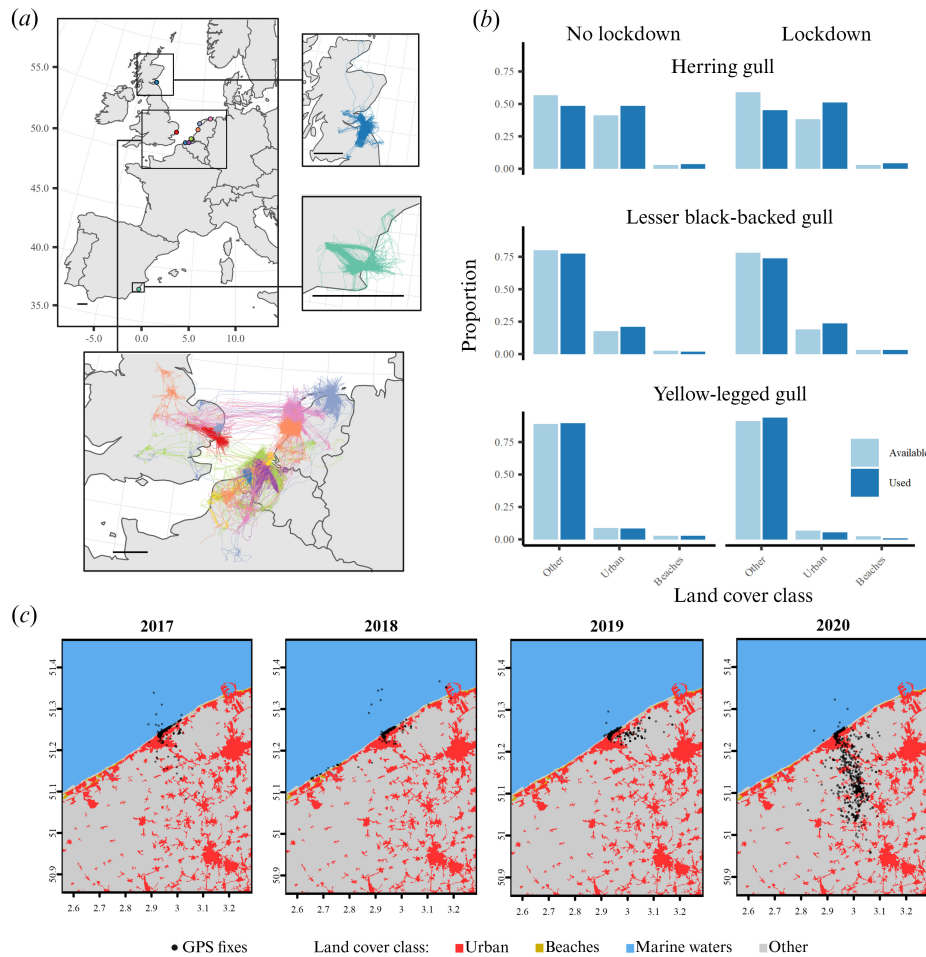


Figure 1. GPS tracking data from three species of gull (herring gull *Larus argentatus*, lesser black-backed gull *L. fuscus* and yellow-legged gull *L. michahellis*) in western Europe, collected during June–July over multiple years (2015–2022), were analysed to compare habitat selection between lockdown and non-lockdown years. (a) Maps (Lambert azimuthal equal area projection) showing colony locations and tracks of 113 individual gulls, totalling 4 75 738 resampled GPS fixes for 353 bird-years (data used in analyses, after processing). Colonies are colour-coded (same colours as in figures 2,3), and the scale bars represent 100 km. (b) The proportion of used (movement step end points) and available (30 points per actual step) land cover classes summarized for the three study species in ‘no lockdown’ and ‘lockdown’ conditions. (c) CORINE land cover maps (100 m² resolution) for a single herring gull tracked over four consecutive years in Belgium, including 2020 when lockdowns were imposed. Note that marine water is included in the ‘other’ category in analyses but shown here separately to differentiate marine and terrestrial habitats.

types of land cover within the urban environment. For example, lockdown restrictions may have resulted in people living in conurbations increasing their use of urban greenspaces or gardens, while decreasing the use of urban commercial areas. In the UK, observations of gulls increased as human use of parks increased [17], suggesting that in some locations, they altered their fine-scale habitat use in response to changes in human mobility.

It is also conceivable that urban-foraging gulls are not particularly sensitive to the presence of humans. So, any lockdown-induced changes in human mobility would have had little or no impact on their movement patterns, as gulls were likely able to utilize urban environments where their preferred anthropogenic food sources were diminished during lockdown, either by switching to alternative anthropogenic resources or by increasing the proportion of natural food items in their diet (see list above). For example, herring gulls can opportunistically prey upon birds (both chicks and adults) [53] and regularly forage on invertebrates, such as earthworms [54] or bivalves [55]—resources that should have remained available regardless of changes in human mobility levels. Interestingly, diversity in the diet of a population of yellow-legged gull chicks in Barcelona, Spain, was lower during lockdown, suggesting that they adapted to changes in human-associated foraging opportunities [56]. In some urban areas, anthropogenic food resources were likely still available; for example, gulls are intentionally fed by humans year-round in Amsterdam [57], and these subsidies continued to some extent during lockdown (J. Shamoun-Baranes, pers. comm.). It is possible that these resources in urban areas increased during lockdown, which could explain the two cases where we observed increased selection for urban land cover. Alternatively, gulls from these colonies may in fact have responded to reduced human disturbance during lockdowns, utilizing key areas for roosting or foraging on refuse bags, which were still being produced during lockdown. In addition, gulls from both of these colonies forage in Belgium where reduced fishing activities were observed during lockdown (electronic supplementary material, table S21), which may have forced birds to utilize urban areas more.

The change in selection for beaches also varied between colonies and may be explained by several factors. Increased selection could be a consequence of: fewer people using beaches during lockdown, reducing disturbance levels; more people using beaches during lockdown, creating additional foraging opportunities; or gulls switching to foraging in beach habitats during lockdown because of increased disturbance or reduced food availability elsewhere, irrespective of whether human beach use

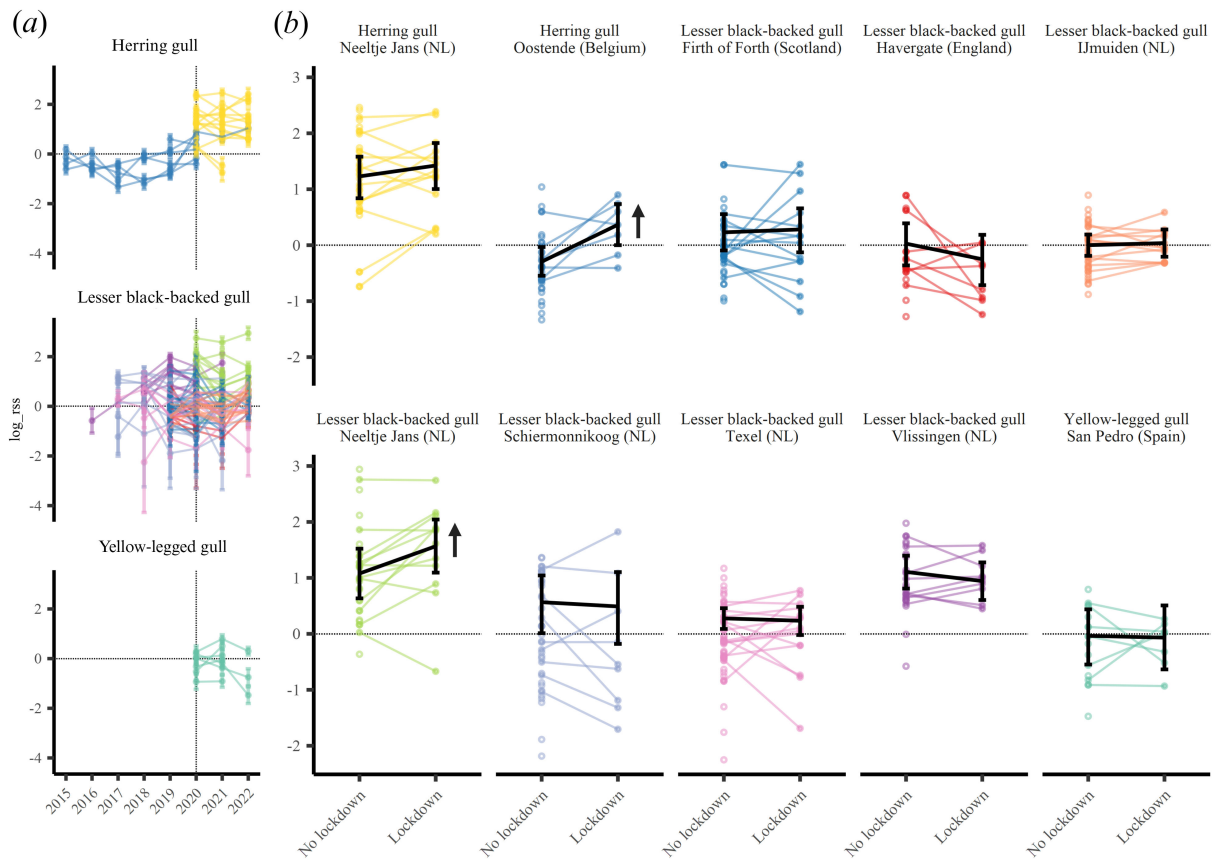


Figure 2. Selection for urban land cover increased for herring gulls in Oostende, Belgium and lesser black-backed gulls in Neeltje Jans, Netherlands, during the pandemic lockdown (2020, vertical dotted line), compared to non-lockdown years. (a) Log relative selection strength (\log -RSS) values for three gull species across multiple years. Each point was estimated from a separate integrated step selection analysis (iSSA) model. Solid lines join point estimates for individual gulls. Colours represent different colonies (same colours as in figure 1a). Error bars are 95% confidence intervals. (b) Log-RSS values for the non-lockdown baseline and the lockdown year (2020). For the ‘no lockdown’ category, hollow points show the separate year estimates for each individual; the solid point shows the mean value for each individual; and the lines join the mean ‘no lockdown’ and ‘lockdown’ values. The black points show colony-level estimates from a linear mixed-effects model. Error bars are 95% CIs. Arrows highlight cases where there is statistical support for a change in habitat selection between ‘no lockdown’ and ‘lockdown’.

had changed [58]. The increase in selection for beaches in the lesser black-backed gull colony in Havergate, England, may have been related to a decrease in disturbance on the beach adjacent to the colony because we detected two potential nest locations in this area in 2020, but none in 2019 (although these may represent loafing locations, rather than nests); unlike many other beaches in the UK during lockdown (electronic supplementary material, table S21), this beach did not see a large increase in human use as it is part of a nature reserve where access was prohibited during 2020, but not in non-lockdown years (electronic supplementary material, table S21). The decrease in selection for beaches for the lesser black-backed gull colony in Schiermonnikoog, the Netherlands, and the yellow-legged gull colony in San Pedro, Spain, may be a consequence of reduced human presence on beaches and thus human food sources. That said, the colonies investigated in our study used beaches relatively little in general, so these findings may be less ecologically important than those revealed by our analyses of urban habitat selection.

(b) Study limitations

It is important to acknowledge that we only assessed gulls’ habitat selection based on broad land cover types and that changes may have occurred at finer spatial scales (e.g. within land cover types) or in other aspects of their behaviour, such as diel activity patterns [19,59,60]. Furthermore, our chosen metric, habitat selection, can vary depending on whether a bird is breeding or not [61–63]. We attempted to understand if our results were sensitive to biases related to the breeding status of birds in our sample, by using GPS fixes to identify potential nest locations, and by ensuring that the periods compared between years matched for each individual. Overall, these checks indicated that our findings were not the result of inter-annual differences in breeding behaviour.

Another limitation is that suitable fine-scale human mobility data were not readily available for analysis, which is a well-recognized problem in the study of human–wildlife interactions [64,65]. Access to human mobility data would have allowed us to link gulls’ habitat selection directly to changes in the environmental presence of humans, potentially resolving complex lockdown dynamics, with overall regional decreases in human mobility and some localized spikes [10]. That said, our innovative use of multiple baseline years (see next section) considerably strengthened our ability to establish causal links between gull movement behaviour and human mobility levels, compared to earlier studies that limited analyses to a contrast

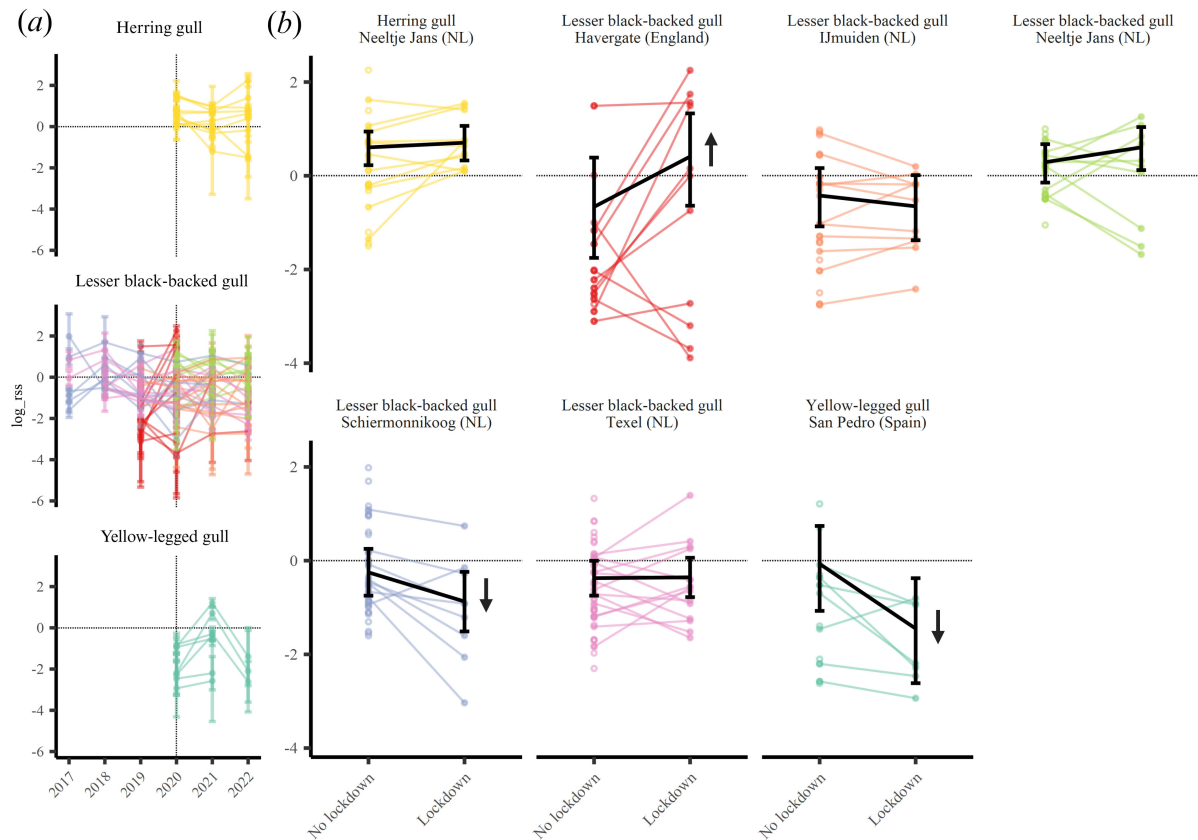


Figure 3. Selection for beach land cover increased for lesser black-backed gulls in Havergate, England, and decreased for lesser black-backed gulls in Schiermonnikoog, the Netherlands, and yellow-legged gulls in San Pedro, Spain, during the COVID-19 pandemic lockdown (2020, vertical dotted line), compared to non-lockdown years. (a) Log relative selection strength (log-RSS) values for three gull species across multiple years. Each point was estimated from a separate integrated step selection analysis (iSSA) model. Solid lines join point estimates for individual gulls. Colours represent different colonies (same colours as in figure 1a). Error bars are 95% confidence intervals. (b) Log-RSS values for the non-lockdown baseline and the lockdown year (2020). For the 'no lockdown' category, hollow points show the separate year estimates for each individual; the solid point shows the mean value for each individual; and the lines join the mean 'no lockdown' and 'lockdown' values. The black points show colony-level estimates from a linear mixed-effects model. Error bars are 95% CIs. Arrows highlight cases where there is statistical support for a change in habitat selection between 'no lockdown' and 'lockdown'.

between just 2 years (typically 2019 and 2020). We also were able to leverage local knowledge of lockdown impacts and gull behaviour to shine some light on the observed context dependence in responses.

Finally, we wish to note that comparisons across species should be conducted cautiously at this stage, given the high degree of between-colony variation observed and our limited sample for yellow-legged gulls, with just seven individuals from a single colony investigated. It would be exciting if our analyses could be extended to other species and colonies using additional datasets that may exist but that we were unaware of, despite our best efforts.

(c) Concluding remarks

Our study constitutes a notable advance in investigating human–wildlife interactions in general, and wildlife responses to COVID-19 lockdowns in particular. First of all, we chose a study system where it is possible to achieve a good degree of replication—across species, countries and breeding locations—and explore animals' change in habitat selection at the rural–urban and marine–terrestrial interface. Analytically, our use of iSSAs allowed us to investigate behavioural choices of animal movement (i.e. habitat selection), rather than emergent patterns (e.g. distance moved). This approach affords crucial mechanistic insight into human–wildlife interactions, setting the scene for parametrizing predictive models capable of forecasting wildlife responses to future habitat degradation and potential conservation interventions [66,67]. Importantly, our study is, to the best of our knowledge, the first to compare animal movement during peak lockdown (in 2020) to baseline data from multiple (non-lockdown) control years (2015–2019, 2021–2022)—allowing more confident identification of true lockdown effects against the background of typical inter-annual variability.

Our findings highlight that generalist species exhibiting high degrees of behavioural and dietary plasticity, such as gulls, are able to cope well with significant changes in human mobility and any associated effects on disturbance levels and resource availability. Identifying why some species thrive in human-modified landscapes, while others struggle, is an urgent research challenge. A detailed mechanistic understanding of how wildlife is affected by anthropogenic activity is essential for mitigating future impacts. Carefully designed research programmes studying animal movement across gradients of urbanization and human disturbance are needed to inform the development of innovative strategies for sustainable human–wildlife coexistence.

Ethics. The COVID-19 Bio-Logging Initiative received approval for secondary data usage from the School of Biology Ethics Committee, University of St Andrews, UK (PI: C.R.; reference: SEC21011; date approved: 9 March 2021). Electronic supplementary material, table S1, provides details of approvals and licenses for the nine studies contributing data to the gull subproject, whose findings are reported here.

Data accessibility. Data and code supporting the paper are available at Zenodo [68]. Electronic supplementary material, table S1 describes the repository and dataset IDs for the GPS tracking data used in this study.

Supplementary material is available online [69].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. R.P.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, software, visualization, writing—original draft, writing—review and editing; B.J.S.: methodology, writing—review and editing; C.B.T.: data curation, methodology, resources, writing—review and editing; N.H.K.B.: methodology, resources, writing—review and editing; B.H.F.: methodology, writing—review and editing; S.W.Y.: methodology, writing—review and editing; R.Y.O.: methodology, writing—review and editing; D.E.-S.: methodology, writing—review and editing; M.A.T.: methodology, writing—review and editing; A.L.: methodology, writing—review and editing; J.S.: data curation, writing—review and editing; F.O.: data curation, writing—review and editing; G.D.C.: data curation, resources, writing—review and editing; K.C.J.C.: resources, writing—review and editing; P.D.: data curation, resources, writing—review and editing; R.R.: data curation, resources, writing—review and editing; J.G.-S.: resources, writing—review and editing; R.M.W.G.: data curation, resources, writing—review and editing; E.M.H.: resources, writing—review and editing; D.T.J.: resources, writing—review and editing; L.L.: resources, writing—review and editing; W.M.: resources, writing—review and editing; N.J.O.: data curation, resources, writing—review and editing; F.R.: resources, writing—review and editing; Á.S.: resources, writing—review and editing; J.S.-B.: data curation, resources, writing—review and editing; E.W.M.S.: resources, writing—review and editing; F.V.: resources, writing—review and editing; C.R.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, visualization, writing—original draft, writing—review and editing.

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

Authors' Notes. After our article was accepted, a study was published that used GPS tracking data to investigate habitat selection of red kites during COVID-19 lockdowns, using baseline data from multiple (non-lockdown) control years [70].

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

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