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Integrating human mobility and animal movement data reveals complex space-use between humans and white-tailed deer in urban environments

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Human expansion into wildlife habitats has increased the need to understand human–wildlife interactions, necessitating interdisciplinary approaches to assess zoonotic disease transmission risks and public health impacts. This study integrated fine-grained human foot traffic data with hourly GPS data from 38 white-tailed deer (*Odocoileus virginianus*), a species linked to SARS-CoV-2, brucella, and chronic wasting disease, in Howard County, Maryland. We explored spatial and temporal overlap between human and deer activity over 24 months (2018–2019) across a hexagonal tessellation with metrics like hourly popularity and visit counts. Negative binomial models were fitted to the visit counts of each deer and humans per tessellation area, using landscape features as predictors. A separate deer-only model included commercial human activity as another predictor. Spatial analysis showed deer and humans sharing spaces in the study area, with results indicating deer using more populated residential areas and areas with commercial activity. Temporal analysis showed deer avoiding commercial spaces during daytime but using them in late evening and early morning. These findings highlight the complex space use between species and the importance of integrating detailed human mobility and animal movement data when managing wildlife–human conflict and zoonotic disease transmission, particularly in urban areas with a high probability of deer–human interactions.

Recently, the increasing encroachment of human populations into wildlife habitats due to demand for land has highlighted the need for a deeper understanding of human–wildlife interactions. Such interactions are important for managing human impacts on wildlife habitats and mitigating the potential for zoonotic disease transmission and novel infectious disease risks. An interdisciplinary approach integrating human mobility science and animal movement ecology to contextualize human–wildlife interactions is a promising research direction to address such problems[1,2].

Traditionally, studies integrating these fields use coarse-grained, large-scale, and static indices like the Human Footprint Index[3] and Human Modification Map[4]. These indices help assess wilderness loss, guide conservation, and predict wildlife responses to human encroachment[5–8]. Lately, these studies have been complemented by those incorporating fine-grained human mobility and animal movement datasets, improving understanding of behaviors and interactions over space and time.

The COVID-19 pandemic offered a unique opportunity to study wildlife responses to human absence during lockdowns[9]. Studies revealed diverse ecological impacts: common murres (*Uria aalge*) became more vulnerable to predation by other bird species[10], while the space use of white sharks (*Carcharodon carcharias*) remained unchanged[11]. Bobcats (*Lynx rufus*)[12] and other mammalian species[13] also showed changes in habitat use.

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During the COVID-19 pandemic, commercial human mobility datasets were made available to researchers. Many provided *COVID-19 human mobility change measures* relative to pre-pandemic baselines[14]. For example, Apple Mobility Trends Reports[15] measures mobile direction request changes, while Google COVID-19 Community Mobility Reports[16] records changes in time spent at points of interest (POIs). These datasets, among others (Strava[17] and iNaturalist[18]), helped assess potential changes in movement and behavior during the pandemic in mountain lions (*Puma concolor*)[19,20] and birds[21], as well as declines in human–wildlife conflicts[22]. However, a key challenge remains: the limited availability of datasets capturing both human and animal movement at the same location and time[23].

While many early human mobility datasets made available during the pandemic are no longer maintained, several remain available for studying human–wildlife interactions. Dewey Data[24] is a company that provides academic researchers with datasets such as Advan Patterns[25] (formerly SafeGraph Patterns), offering human foot traffic data dating back to 2018 that quantifies the number of people visiting specific POIs over time. While providing new opportunities for studying human–wildlife interactions, the ecological research potential of these datasets remains largely untapped, possibly due to unfamiliarity and integration challenges with traditional ecological data.

This study aims to demonstrate the potential of utilizing human foot traffic datasets while addressing their limitations and contributing to research integrating animal movement and human mobility. As a case study, we use Advan foot traffic data and GPS-collared white-tailed deer (*Odocoileus virginianus*) data—a species found to be infected with SARS-CoV-2[26]—to examine human-deer interactions in Howard County, Maryland. We compute the monthly count of visits (visit count) and the number of visits each month over each hour (popularity by hour) from January 2018–December 2019 across a hexagonal tessellation in a primarily urban[27] study area. Monthly visit counts are regressed against a set of landscape variables. To the best of our knowledge, this is the first attempt combining Advan foot traffic data with detailed animal movement data, setting a precedent for future research.

Results
Mobility patterns
One of the key challenges of this analysis was to compare mobility patterns from deer and humans using datasets that have very different data structures. Deer data are captured as discrete trajectories while human data are captured as visits to POIs. Therefore, both datasets were aggregated to a single tessellation of hexagons within the 100% minimum convex polygon (MCP) encompassing the deer home ranges (Fig. 1). This resulting study area included several Howard County parks, residential buildings, and 739 commercial POIs (Fig. 1). Hexagons within each Howard County park were merged into single units, resulting in 704 distinct polygons, including individual hexagons and merged park regions (Fig. 1). Each tessellation polygon was characterized by monthly counts of deer and human visits from January 2018 to December 2019 (24 months), yielding a total of 16,896 observation pairs. Additionally, each polygon was described by an array of visits over 24 h, summarized for each month for both deer and humans, referred to as "popularity by hour" and yielding 16,896 pairs of popularity arrays.

Visit count
We calculated the monthly mean counts for deer and commercial human visits from January 2018–December 2019 for each tessellation polygon (Fig. 2a, b). The mean visit count for deer was 3.6 (s.d. = ±17.5) across the 24 months, with a maximum visit count of 776. For humans, the mean commercial visit count was 315.4 (s.d. = ±1509.8), with a maximum commercial visit count of 37,035. Within the observation pairs (tessellation polygon and month) (N = 16,896), 82% (n = 13,937) of the observations had zero deer visits and 68% (n = 11,517) of the observations had zero commercial human visits. Furthermore, 6.3% (n = 1059) of observations had both deer and commercial human visits, while 11% (n = 1900) had deer visits, but no commercial human visits, and 26% (n = 4320) had commercial human visits, but no deer visits.

Deer visits were naturally highest in the Howard County parks where they were captured, however, they also tended to move into the local residential and commercial neighborhoods surrounding the parks (Fig. 2a). Human visits to the local parks and commercial POIs were captured in the Advan dataset, and highlighted areas with commercial human activity (Fig. 2b). We also calculated the mean of deer and commercial human visit counts for winter (December, January, February) and summer (June, July, August) from January 2018 to December 2019 for each tessellation polygon (Fig. 2c–f). Deer visited areas outside of county parks more frequently in the winter (Fig. 2c) than in the summer (Fig. 2e). Parks had fewer commercial human visits in the winter (Fig. 2d) than in the summer (Fig. 2f). Thus, both deer and humans exhibited seasonal variations in their visits across the landscape.

We also examined the monthly mean visit counts for deer and humans over the 24-month period, averaged across three landscape types including: (1) parks where deer were captured and other Howard County parks, (2) locations with commercial human activity, and (3) locations without commercial human activity. We note that areas with commercial human activity may contain a mix of residential and commercial land use with varying intensity as well as unmanaged green space. Locations with no commercial activity may contain a mix of residential land use and unmanaged green space. As expected, county parks had the highest monthly deer visits, with a mean of 76.2 (s.d. = ±100.9) and a maximum of 776 visits. In comparison, areas with commercial activity had the lowest monthly deer visits, with a mean of 1.9 (s.d. = ±5.6) and a maximum of 158. Areas without commercial activity had moderate monthly deer visits, averaging 2.5 (s.d. = ±8.3), with a maximum of 216. For commercial human visits, parks had monthly visits averaging 667.3 (s.d. = ±961.6), with a maximum of 6934. Areas with commercial activity had higher monthly commercial human visits than parks, with a mean of 982 (s.d. = ±2582.1) and a maximum of 37,035.
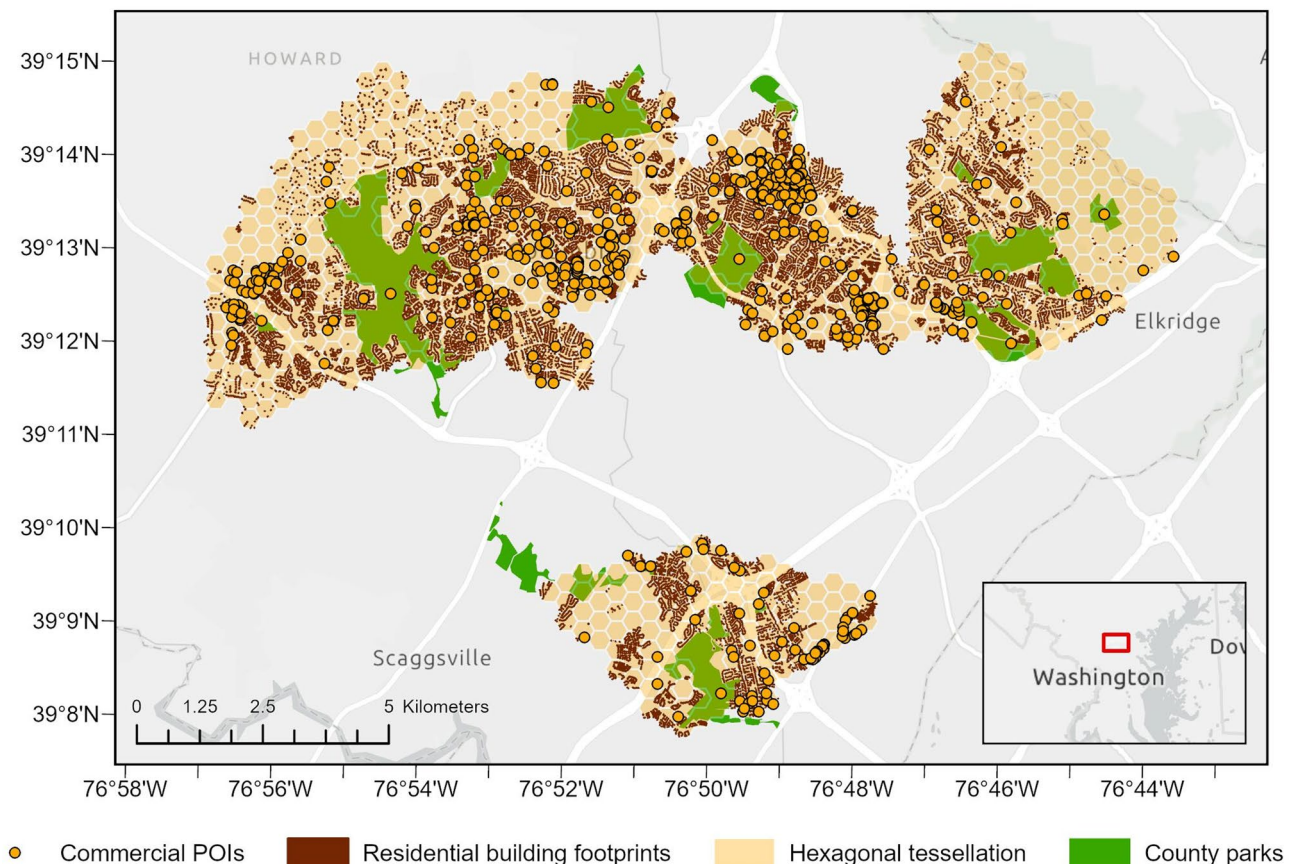
Fig. 1. Study area in Howard County, Maryland, defined by a hexagonal tessellation (tan hexagons) within the 100% MCP of deer home ranges, showing commercial POIs (orange points), residential building footprints (brown polygons), and county parks (green polygons). Hexagons within each Howard County park were merged into single polygons. Map was created using ArcGIS Pro 3.3.2 (basemap[28] source: County of Anne Arundel, VGIN, Esri, TomTom, Garmin, SafeGraph, FAO, METI/NASA, USGS, EPA, NPS, USFWS, USDA, M-NCPPC, NOAA).

Popularity by hour

Popularity by hour can provide information about the daily activity patterns of both deer and humans relative to one another. We calculated the mean popularity by hour for each of the three different landscape types—parks, areas with commercial activity, and areas without commercial activity—for deer and humans from January 2018–December 2019 (Fig. 3). Parks were most popular for deer during the day (7:00–22:00 h) (Fig. 3a). In the evening to early morning (22:00–7:00 h), parks decreased in popularity for deer while nearly doubled in commercial areas at a time with less human activity (Fig. 3a, b). The popularity of areas without commercial activity for deer remained relatively consistent, increasing very slightly in the afternoon when people were in commercial areas (12:00–17:00 h) (Fig. 3c).

We compared the mean popularity by hour of the three different landscape types for deer and humans during the winter and summer (Fig. 4). On average, parks were only half as popular for deer in winter compared to summer (Fig. 4a, b), likely due to a reduction in resources. This decline was especially evident in evening hours, when deer shifted their activity toward commercial areas (Fig. 4c, d). Areas without commercial activity, in contrast, showed increased popularity during winter afternoons compared to summer (Fig. 4e, f), possibly because they offer greater safety and more reliable food sources during this time of year. These seasonal patterns highlight the influence of resource availability and environmental conditions on deer behavior.

Statistical model findings

To contextualize the way in which humans and deer share the landscape, we regressed the monthly visit counts per tessellation area against a set of landscape variables including nighttime human population density, mean daytime temperature, natural habitat connectedness, commercial human activity, residential and commercial building area, road density, and available habitat (Fig. 5). We also modeled deer activity independently and included commercial human activity as an independent variable (Fig. 5a). We found that as human nighttime population density, commercial human activity, and residential building area increased, deer activity also increased (Fig. 5a, b). Conversely, as mean daytime temperatures, natural habitat connectedness, commercial
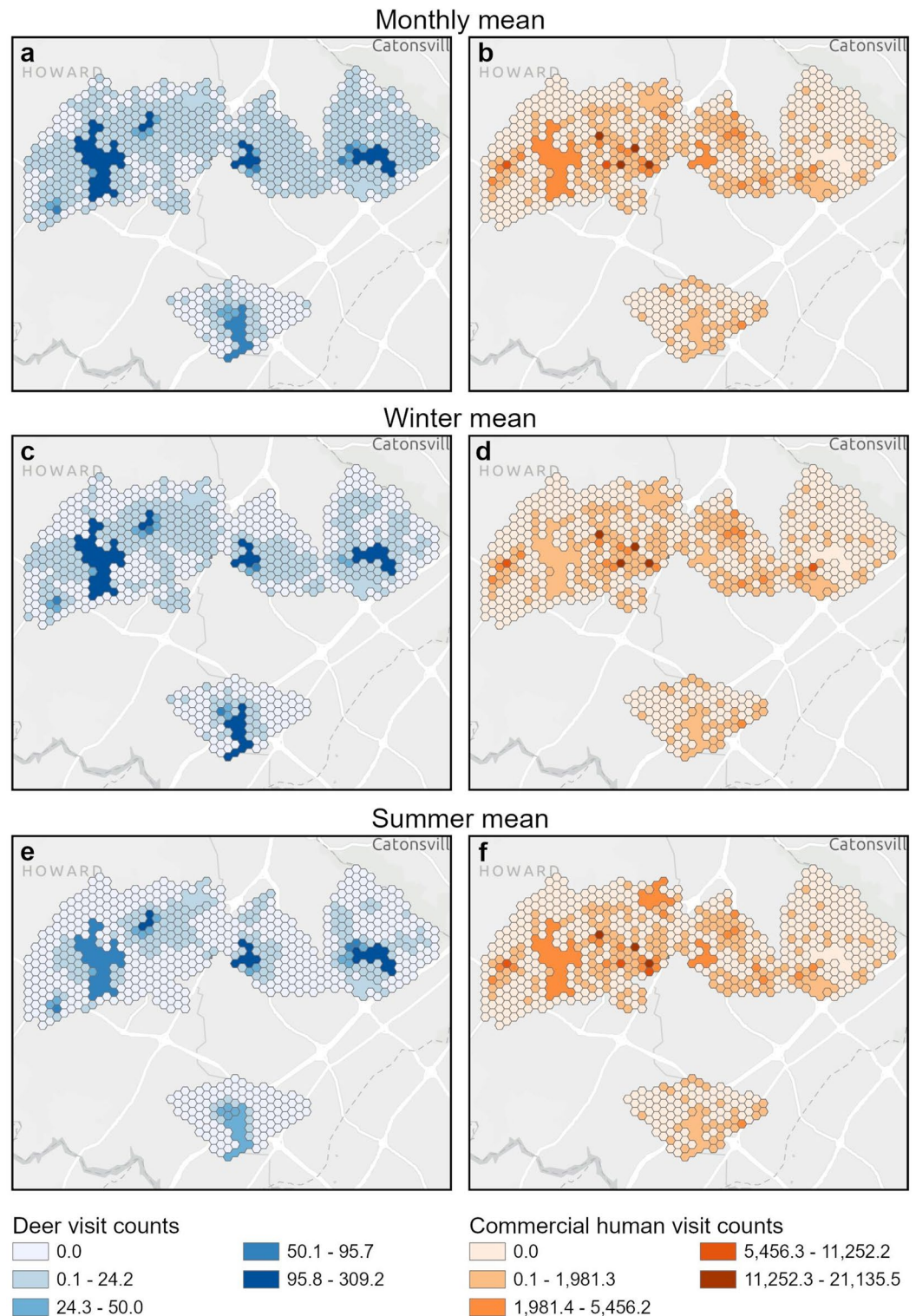
Fig. 2. Mean visit counts of deer (blue) and humans (orange) in the hexagonal tessellation from January 2018 to December 2019, with hexagons within each Howard County park merged into larger park polygons (**a–f**). Monthly mean visit counts of deer (**a**) and humans (**b**). Winter mean visit counts of deer (**c**) and humans (**d**). Summer mean visit counts of deer (**e**) and humans (**f**). Maps were created using ArcGIS Pro 3.3.2 (basemap[28] source: County of Anne Arundel, VGIN, Esri, TomTom, Garmin, SafeGraph, FAO, METI/NASA, USGS, EPA, NPS, USFWS).
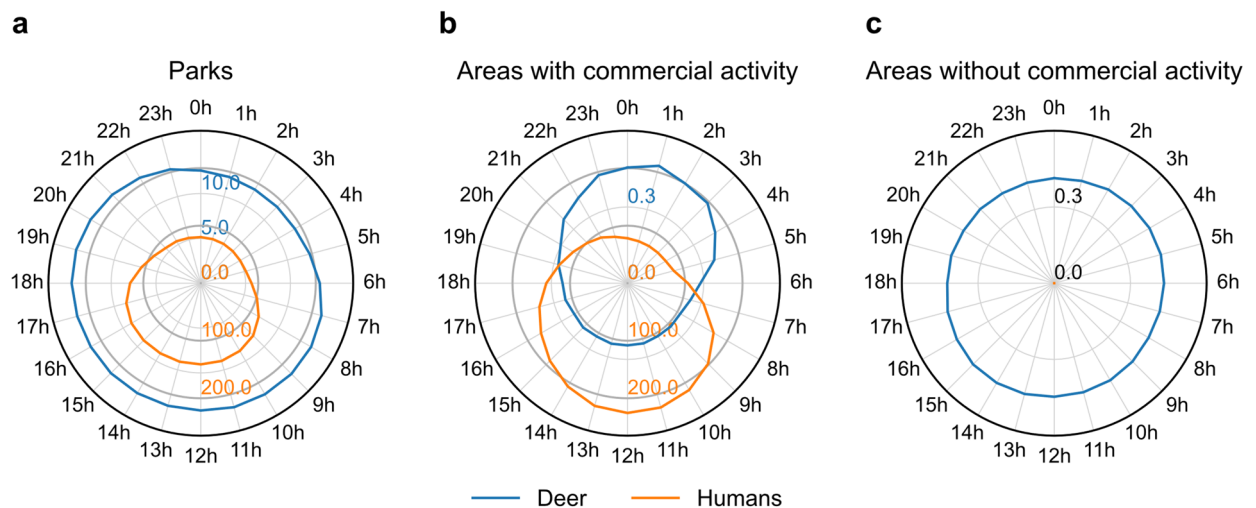
Fig. 3. Mean popularity by hour of deer (blue line) and humans (orange line) in parks (**a**), areas with commercial activity (**b**), and areas without commercial activity (**c**) from January 2018 to December 2019. The values were smoothed using a 3-h rolling mean.

building area, and road density increased, deer activity decreased (Fig. 5a, b). The availability of habitat did not appear to be a significant predictor of deer activity (95% credible intervals overlapped 0).

We also found that as nighttime population density increased, commercial human activity increased (Fig. 5b). This likely means that when more people live within a specific local area, they are contributing to the local commercial activity, especially in regions that are mixed commercial and residential use as seen in highly urban areas. Naturally, as commercial building areas increased, commercial human activity increased. Yet, as habitat connectedness, residential building area, road density, and available habitat increased, commercial human activity decreased (Fig. 5b). Temperature was not a significant predictor of commercial human activity.

Discussion

In this study, we integrated human mobility and deer movement data using the case study of Howard County, Maryland. The analysis of such data allows us to understand where and when humans and deer may come into contact and to better contextualize these interactions. We found that deer and humans share the same developed spaces outside of the parks where deer were captured. For example, our models showed that deer preferred residential areas that were more populated (more single-family homes per unit area or multi-family residences). However, we found lower deer activity in commercial areas, indicating that deer may be avoiding areas that are highly urbanized city centers. In fact, both deer and humans seemed to avoid areas with high road density. While the analysis of deer and human monthly visits across the study area suggests that humans and deer share the same spaces, the finer scale temporal analysis showed that deer typically avoided commercial spaces at times when human activity there was high, but possibly utilized resources found in these spaces, as well as residential yards, in the late evening and early morning, especially in the winter months.

Our findings were able to better characterize initial findings observed previously[29]. Specifically, while deer were attracted to areas where there was commercial human activity, our models showed that deer activity decreased in areas where commercial building footprint area was large. This initially seemed ecologically conflicting because commercial human activity and commercial building footprint area were correlated. However, this complex set of relationships likely emerges from the different types or characteristics of "commercial POIs" visited by humans in the Advan dataset. Commercial POIs range from those located in dense commercial areas where you would naturally find more impervious surfaces and, therefore, fewer deer (e.g., shopping malls and restaurants), to those located in more residential areas with more yards and manicured grassy areas around the buildings themselves where deer are commonly found (e.g., golf courses, schools, cemeteries). However, these larger manicured areas around buildings that are dominated by turfgrass were not included in our categorization of habitat patches, yet may serve as habitat for urban deer. This may also help to explain the unexpected negative relationship between deer activity and habitat connectedness and a lack of correlation between available habitat and deer activity. Future work should explore the nuances in these different types of habitats surrounding commercial POIs and residential areas and their relationship to deer activity.

Following the vision of Ellis-Soto et al.[1], this study among other recent work[30] highlights the potential of utilizing human foot traffic datasets to foster new research that integrates animal movement ecology and human mobility science. However, integrating human foot traffic data with wildlife GPS data is not without its challenges as these datasets can have different data structures. Human foot traffic data such as Advan Patterns is created by aggregating a set of individual trajectories to mobility measures tied to specific areas or point locations. This makes it easy to both protect the privacy of users, comply with regulations on sharing personal data, and to
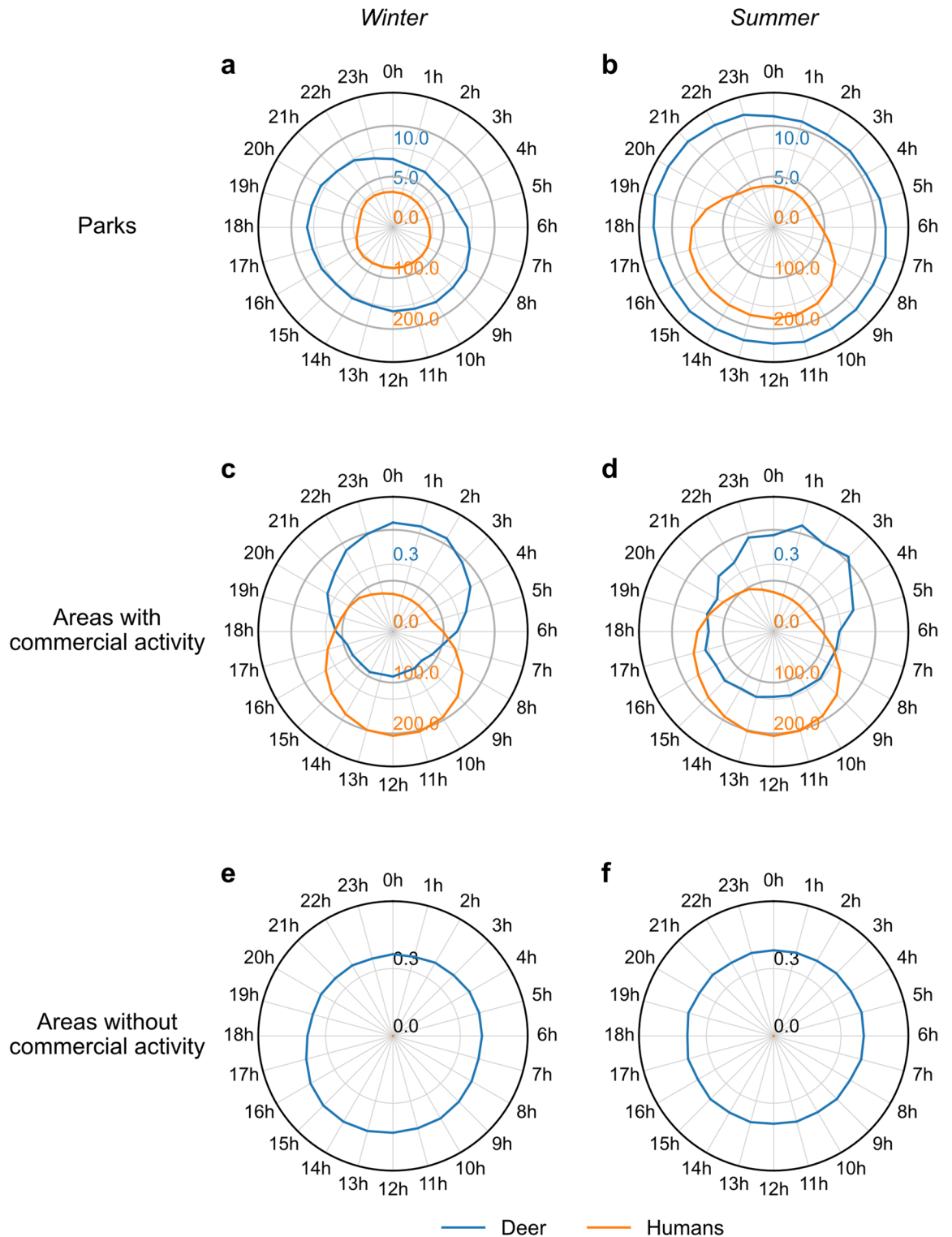
Fig. 4. Mean popularity by hour of deer (blue line) and humans (orange line) during winter and summer in parks (**a,b**), areas with commercial activity (**c,d**), and areas without commercial activity (**e,f**) from January 2018 to December 2019. The values were smoothed using a 3-hour rolling mean.

reduce complexity for analysis. While pseudonymous human trajectory data is available from companies like Veraset[31], it is prohibitively expensive and less accessible to those doing ecological research. On the other hand, wildlife GPS data provides the raw locations of tracked wildlife at specific time stamps. To enable meaningful comparisons that could shed light on deer-human interactions, deer GPS data were aggregated to match the metrics available in the Advan data using a tessellation of hexagons. However, this process is subject to the
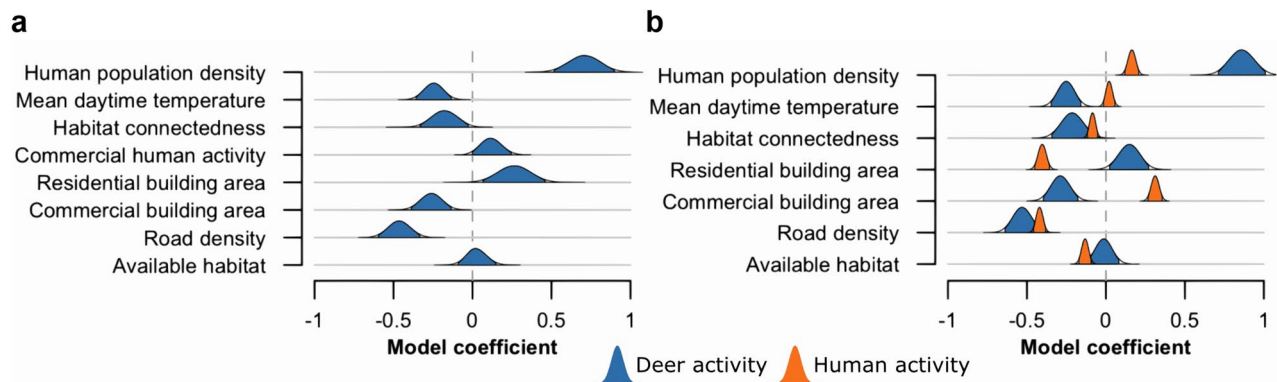
Fig. 5. Posterior distributions of estimated model coefficients from models predicting deer (blue) (**a**,**b**) and human (orange) (**b**) activity. Outlined distributions represent all values in the posterior distribution and colored areas represent the 95% credible intervals.

Modifiable Areal Unit Problem (MAUP), where the choice of spatial units can influence results. Intuitively, a larger tessellation would reduce the ability to capture detailed interaction patterns, and a smaller tessellation would mean that there would be few hexagons with both human and wildlife observations.

Additionally, we found that it was necessary to merge hexagons that make up county parks due to differences in how human mobility and deer movement data is structured. Advan data aggregates human visits to a single park POI, which is associated with just one hexagon within the park, regardless of the park's overall size. In contrast, deer GPS data recorded visits across multiple hexagons within the same park. This initial mismatch created challenges for analysis, particularly the regression models, as only one hexagon in each park contained both deer and human visits, while the remaining hexagons were characterized solely by deer visits. Future work should explore automated approaches for merging hexagons in other large areas with similar challenges, such as golf courses, schools, or cemeteries, to enhance analysis.

Human foot traffic data presents several challenges related to availability, coverage, errors, and representativeness. While free and publicly available during the onset of the pandemic, Advan data among other foot traffic datasets are now only available to researchers for a monetary fee. Geographic coverage of such data can vary across regions and time, limiting its utility for comprehensive or longitudinal studies. The persistence of attributes over time is also not guaranteed. For example, Advan phased out the human mobility measure that captured the average distance travelled from a user's home location to each POI in 2023. These business-oriented decisions can reduce the reproducibility of studies over time. Finally, Advan primarily captures visits from individuals carrying mobile devices with location services enabled, potentially underrepresenting specific demographics, such as older adults or those with privacy concerns. These limitations necessitate careful consideration when interpreting results.

Despite these limitations, human foot traffic data like Advan remains one of the most granular and rich data available capturing human mobility. We demonstrated the potential of using such datasets to investigate deer-human interactions, using only two of the many metrics available. Future work may investigate how other measures of human mobility (e.g., dwell time, unique visitors, human mobility flow) could be used to generate insights into human mobility and animal movements to estimate potential interactions. Most human foot traffic data are limited to commercial POIs to protect user privacy. Therefore, for this study, alternative data sources had to be used to characterize residential human activity. For this, we used detailed human population counts (100 m x 100 m resolution) as a proxy for "visit count" to residential POIs. We also used residential building footprint area to get a better understanding of how residential areas and human activity in these areas relate to deer activity. Future work could incorporate the National Household Travel Survey[32] to better understand the "popularity by hour" in residential areas.

In conclusion, we explored the potential of integrating human mobility and animal movement data. Our findings are twofold: revealing the complex nature of space utilization between deer and humans in urban settings and providing a foothold for future studies that aim to combine human foot traffic data with detailed animal movement data. Such studies can facilitate a more detailed understanding of behaviors and interactions between wildlife and human populations over space and time. These types of studies would be broadly useful for applications related to wildlife-human conflicts, conservation, and epidemiology. More importantly, understanding human–wildlife interactions is especially crucial for intervention and prevention of emerging zoonotic diseases, especially where close contact between wildlife and humans facilitates transmission of zoonotic pathogens.

Methods

The deer trapping protocol was approved by the Animal Care and Use Committee (IACUC approval #16-024) of the United States Department of Agriculture Beltsville Agricultural Research Center. All methods were carried out in accordance with relevant guidelines and regulations.
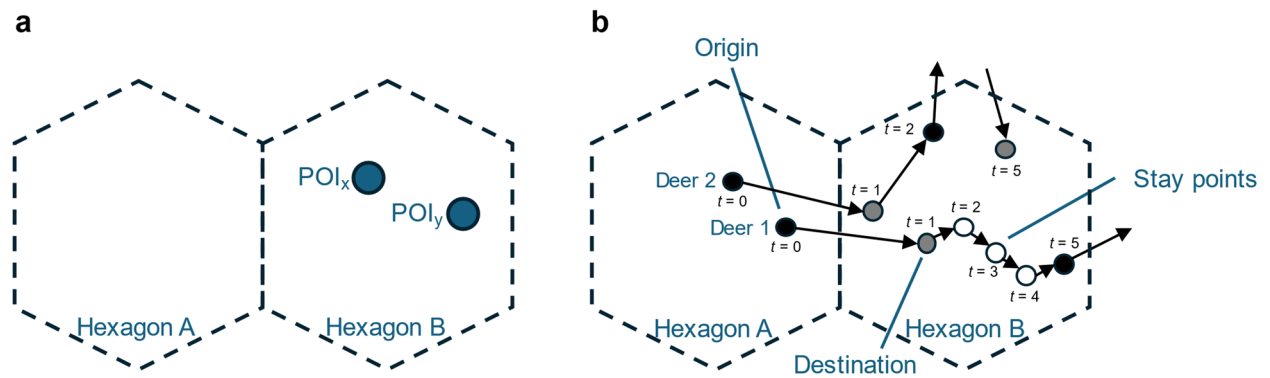
Fig. 6. Visualization of the hexagonal tessellation showing POIs within a hexagon (**a**) and deer movement trajectories across the tessellation (**b**).

Mobility and movement data and metrics

Mobility and movement data

The study uses GPS data capturing the movement of deer and human foot traffic data to characterize human mobility in Howard County, Maryland. Deer were captured and fitted with GPS collars in five Howard County parks, namely Blandair Regional Park, Cedar Lane Park, Middle Patuxent Environmental Area, Rockburn Branch Park, and Wincopin Trails System[29]. In this study, we used a subset of this GPS collar data, capturing the location of 38 deer each hour from January 2018 to December 2019 for 187,838 observations.

Human foot traffic data was collected from Dewey Data[24] including both the SafeGraph Places and Advan Monthly Patterns datasets[25]. The Places dataset comprises the point geometry for millions of public POIs in the U.S., such as parks, restaurants, and schools, of which 4,346 POIs fall within Howard County, Maryland. The Patterns dataset provides various metrics capturing human foot traffic at each POI from January 2018–December 2019, derived from GPS trajectories, aggregated into weekly or monthly patterns. We note that these data do not capture mobility patterns associated with private or residential places. In this study, two monthly patterns were used to characterize human mobility associated with commercial POIs including *raw_visit_count* and *popularity_by_hour*. Raw visits refer to the total count of visits to each POI each month, including re-occurring visits. For example, in January 2018, the Metro by T Mobile Authorized Dealer at 5865 Robert Oliver Place in Howard County, Maryland, had 18 visits. Hourly popularity is the number of visits in each hour over the month. In the case of Metro by T Mobile, the popularity for the month of January 2018 is expressed as an array of 24 h: [0,0,0,0,0,0,0,1,2,3,2,4,2,2,2,2,5,3,3,2,3,2,2,1] where the first element in the array corresponds to the hour of midnight to 1 AM, second is 1 AM to 2 AM, etc.

In the Advan dataset, a single commercial human visit may be associated with multiple POIs due to parent-child relationships among POIs. Specifically, a parent POI may encompass several child POIs, and a visit to a child POI can also be recorded for its parent, resulting in double-counting of visits. For example, Columbia Gateway Plaza is a parent POI that contains the child POIs KinderCare, Flavors of India, and Rudy's Mediterranean Grill. In January 2018, these child POIs recorded 2, 57, and 361 visits, respectively—adding up to 420 visits, which is the same number of visits recorded for their parent POI, Columbia Gateway Plaza, reflecting double-counting of the same visits. To prevent double-counting, child POIs (i.e., those with a parent POI) were removed from the dataset to ensure that commercial visits were counted only once. An exception was made for child POIs of Columbia Association Open Space, which were retained to preserve the spatial granularity of commercial visit data. In this case, the parent POI, Columbia Association Open Space, was removed to avoid redundancy.

Mobility and movement metrics

We computed the visit count and popularity by hour metrics for both deer and humans for a set of hexagons arranged in a tessellation so that the mobility patterns across the landscape could be analyzed and compared. Given the average distance between deer locations and POIs of 356 m, we roughly estimated a hexagon area of 126,736 m^2. Hexagons located within the total deer home range, defined by the 100% MCP, were used as the study area for analysis.

The commercial human visit counts and hourly popularity of each hexagon were calculated as the sum of the visits and hourly popularities of the POIs located within each hexagon. Consider a hexagonal tessellation with POIs in Hexagon B (Fig. 6a). If POI_x has 3 visits and POI_y has 2 visits, Hexagon B will have 5 visits for that month (Fig. 6a). Similarly, popularity for each of the hexagons can be calculated as the total count of visits over 24 h, summed over the month. For example, if POI_x has monthly popularity = [0,0,3,3,2,1, … n] and POI_y has monthly popularity [0,0,0,1,1,2, … m], Hexagon B will have a monthly popularity of [0,0,3,4,3,3, … n + m].

Next, we aggregated the deer GPS data by counting the number of visits and the hourly popularity for each hexagon for each month. For each hexagon and each month, the count of visits increases by one each time a deer is first observed in a hexagon. If the deer left and then returned to the same hexagon within the same month, the count of visits to that hexagon would increase for that month. The hourly popularity for deer was calculated by counting the number of deer visits in each hour over the month.

For instance, in Hexagon B, let us assume that we recorded 8 GPS data points with hourly intervals from two deer, labeled Deer 1 and Deer 2 (Fig. 6b). Deer 1 made a single visit to Hexagon B, while Deer 2 visited twice, leaving and returning within the specified time period. This would result in a total of 3 visits to Hexagon B. Popularity in Hexagon B would be calculated at the hourly time points $t = [1,2,3,4,5]$, with the corresponding values: popularity = [2,2,1,1,2].

In the Advan dataset, parks are captured by a single POI. This is problematic in the analysis because, for most parks, human activity corresponds to just one hexagon, while deer activity corresponds to many hexagons. To address this issue, park hexagons within each of the Howard County parks[33] were merged using an automated process. A hexagon was categorized as a park hexagon if its center fell within the boundaries of a park. Adjacent park hexagons were combined into a single polygon feature. Thus, the aggregation and merging process resulted in 704 polygons. Each tessellation polygon unit can be described by a series of values including deer visit count, commercial human visit count, deer hourly popularity, and commercial human hourly popularity for each of the 24 months from January 2018–December 2019. The calculation of mobility and movement metrics were performed using Python, including the ArcPy package.

Modeling approach

To further explore what landscape characteristic correlated with both deer and commercial human activity, we fit negative binomial models to the visit counts of each deer and humans per tessellation area. For this analysis, we removed tessellation areas that did not contain at least 1 point POI. Therefore, we were left with 227 tessellation areas. We included nighttime human population density, temperature, available habitat, habitat connectedness, residential and commercial building area, and road density as linear predictors in both models. In a separate deer-only model, we also included commercial human activity as a predictor variable.

Landscape features

- *Nighttime human population density*: We used the Estimated U.S. Population 2020 dataset from WorldPop[34] to estimate human population density during nighttime hours. This dataset estimates the U.S. population density at 100 m resolution and is based on population data from the 2020 U.S. Census[35]. Since these data come from U.S. census data, they are capturing people in their place of residence, and we can consider them—spatially—as the local human population before and after commercial hours (or the "nighttime population"). To calculate a nighttime population density for each polygon, we summed the values of all grid cells that intersected a polygon and divided by the area of the respective polygon.
- *Mean monthly temperature*: To calculate the mean monthly temperature, we used the Terra Moderate Resolution Imaging Spectroradiometer (MODIS) Land Surface Temperature/Emissivity 8-day product Version 6.1[36], which we downloaded using the Google Earth Engine Python API package. The MODIS land surface temperature (LST) product provides an average 8-day per-pixel land surface temperature at a 1-km spatial resolution. All pixels were an average of all the corresponding MODIS LST pixels collected within an 8-day period. We chose to average across daytime temperatures and, for each grid cell, we calculated the monthly average of each month that corresponded to the deer sampling period. To calculate an average temperature for each polygon, we took the mean of all monthly average grid cells that intersected a polygon. This variable varied temporally.
- *Available habitat*: We used the Chesapeake Bay Conservancy Land Cover 1 m resolution raster data[37] to calculate the proportion of available habitat in each polygon. Here, we combined the proportion of raster cells classified as a Forest, Natural Succession, or Tree Canopy Other within each polygon using the sf[38] and terra packages in R[39], which we considered as "habitat" cells.
- *Habitat connectedness*: Using the same habitat categories as above, we combined all "habitat" cells connected on at least 1 of 8 sides (Queen's case) into individual habitat patches. We then calculated the mean Contiguity Index[40,41] of habitat patches in each hexagon using the *landscapemetrics* package[42] in R. The Contiguity Index assesses the spatial connectedness of cells in each patch.
- *Residential and commercial building area*: We used the Howard County GIS Buildings Major layer[43], which represents the footprints of buildings with areas of 200 square feet or more, along with the Howard County GIS Land Use layer[44] to estimate the areas of residential and commercial buildings. First, we reclassified the land use categories of the parcels into two land use types: residential and commercial. The residential land use category included Age-Restricted Residential, Apartment, Mobile Home, Single-Family Attached, and Single-Family Detached parcels, while the commercial land use category included Commercial, Government & Institutional, Industrial, and Other Transportation & Utilities parcels. We then performed a spatial join between the building footprints and the corresponding parcels with updated land use categories to classify the buildings as either residential or commercial. Finally, we calculated the total area in square meters of residential and commercial buildings within each polygon.
- *Road density*: To calculate road density in each polygon, we used the U.S. Census Bureau 2023 Tiger/Lines All Roads layer[45] for Howard County, Maryland, and extracted the total length of roads in each polygon and divided that value by the area of the respective polygon.
- *Commercial human activity*: Commercial human activity was used only in the model to analyze deer activity. Here, we used the visit counts of humans per polygon area per month calculated from the Advan[25] dataset. Therefore, this variable varied temporally.

Statistical models

To assess the influence that each landscape characteristic had on deer and commercial human activity, we fit independent negative binomial models to the visit counts of each deer and humans per polygon area. We also

fit a deer-only negative binomial model using the same independent variables and including the commercial human activity variable to explore the influence of human activity on deer habitat use. Since polygon size varied and larger polygons had the opportunity to capture more deer locations, we included the log area of the polygon area as an offset parameter in the linear predictor in both deer models. For the human activity model, we used the log number of POIs within each polygon area as an offset parameter since an increase in POIs provided more opportunity to capture human visits. To use all variables in our model, including those that were correlated, we used a form of Bayesian LASSO regression by giving all model coefficients, excluding the intercept, Laplace priors. The Laplace distribution shrinks values for variables that have low explanatory value toward 0 based on the tuning parameter λ and reduces the variability of estimates when multicollinearity exists[46]. We allowed the model to estimate λ, which was given a Γ(0.001,0.001) prior. The intercepts were given N(0,100) priors and our dispersion parameter was given a Uniform(0,50) prior in each model.

Models were fitted using a Markov Chain Monte Carlo (MCMC) algorithm implemented in Nimble version 0.1.3[47] using the nimble package in R. Four parallel chains were run, each for 35,000 iterations, starting from random starting values. The first 10,000 iterations from each chain were discarded and every other iteration was kept to reduce autocorrelation among the samples. A total of 50,000 iterations were obtained. Model convergence was assessed by checking that the Gelman-Rubin diagnostic statistic[48] for each parameter was < 1.1 and by visually inspecting trace plots of the MCMC samples. We considered a parameter to be significant if the 95% Bayesian credible intervals of the parameter coefficient did not overlap 0.

Data availability

The GitHub repository (https://github.com/szandrapeter/human-mobility-animal-movement-integration) provides the deer GPS data, the empty tessellation for the study area, and the code to generate the tessellated deer visit count and the popularity by hour. The raw human foot traffic data are available from Dewey Data, but restrictions apply to the availability of these data, which were used under license for the current study and so are not publicly available. However, with permission from Dewey, we have made the tessellated human visit count available. The code for the statistical models that use the tessellated deer and human visit count are available in the GitHub repository. Other publicly available data used for the statistical models are cited in the manuscript and/or linked in the GitHub repository.

References

1. Ellis-Soto, D. et al. A vision for incorporating human mobility in the study of human–wildlife interactions. *Nat. Ecol. Evol.* **7**, 1362–1372 (2023).
2. Miller, H. J., Dodge, S., Miller, J. & Bohrer, G. Towards an integrated science of movement: converging research on animal movement ecology and human mobility science. *Int. J. Geogr. Inf. Sci.* **33**, 855–876 (2019).
3. Sanderson, E. W. et al. The human footprint and the last of the wild. *BioScience* **52**, 891 (2002).
4. Kennedy, C. M., Oakleaf, J. R., Theobald, D. M., Baruch-Mordo, S. & Kiesecker, J. Managing the middle: A shift in conservation priorities based on the global human modification gradient. *Glob. Change Biol.* **25**, 811–826 (2019).
5. Watson, J. E. M. et al. Persistent disparities between recent rates of habitat conversion and protection and implications for future global conservation targets. *Conserv. Lett.* **9**, 413–421 (2016).
6. Tucker, M. A. et al. Moving in the anthropocene: global reductions in terrestrial mammalian movements. *Science* **359**, 466–469 (2018).
7. Jones, K. R. et al. One-third of global protected land is under intense human pressure. *Science* **360**, 788–791 (2018).
8. Kühl, H. S. et al. Human impact erodes chimpanzee behavioral diversity. *Science* **363**, 1453–1455 (2019).
9. Rutz, C. et al. COVID-19 lockdown allows researchers to quantify the effects of human activity on wildlife. *Nat. Ecol. Evol.* **4**, 1156–1159 (2020).
10. Hentati-Sundberg, J., Berglund, P. A., Hejdström, A. & Olsson, O. COVID-19 lockdown reveals tourists as seabird guardians. *Biol. Conserv.* **254**, 108950 (2021).
11. Huveneers, C. et al. The power of national acoustic tracking networks to assess the impacts of human activity on marine organisms during the COVID-19 pandemic. *Biol. Conserv.* **256**, 108995 (2021).
12. Procko, M., Naidoo, R., LeMay, V. & Burton, A. C. Human impacts on mammals in and around a protected area before, during, and after COVID-19 lockdowns. *Conservat. Sci. Prac.* **4**, e12743 (2022).
13. Behera, A. K., Kumar, P. R., Priya, M. M., Ramesh, T. & Kalle, R. The impacts of COVID-19 lockdown on wildlife in Deccan Plateau, India. *Sci. Total Environ.* **822**, 153268 (2022).
14. Elarde, J., Kim, J. S., Kavak, H., Züfle, A. & Anderson, T. Change of human mobility during COVID-19: A United States case study. *PLoS ONE.* **16**, e0259031 (2021).
15. Apple. COVID-19 - Mobility trends reports. https://covid19.apple.com/mobility/ (2022). Accessed: 17 March 2025.
16. Google. COVID-19 Community Mobility Reports. https://www.google.com/covid19/mobility. Accessed: 17 March 2025.
17. Strava. Running, Cycling & Hiking App - Train, track & share. https://www.strava.com/. Accessed: 17 March 2025.
18. iNaturalist. A Community for Naturalists. https://www.inaturalist.org. Accessed: 17 March 2025.
19. Wilmers, C. C., Nisi, A. C. & Ranc, N. COVID-19 suppression of human mobility releases mountain lions from a landscape of fear. *Curr. Biol.* **31**, 3952-3955e3 (2021).
20. Vardi, R., Berger-Tal, O. & Roll, U. iNaturalist insights illuminate COVID-19 effects on large mammals in urban centers. *Biol. Conserv.* **254**, 108953 (2021).
21. Mikula, P. et al. Urban birds' tolerance towards humans was largely unaffected by COVID-19 shutdown-induced variation in human presence. *Commun. Biol.* **7**, 874 (2024).
22. Pokorny, B., Cerri, J. & Bužan, E. Wildlife roadkill and COVID-19: A biologically significant, but heterogeneous, reduction. *J. Appl. Ecol.* **59**, 1291–1301 (2022).
23. Robira, B., Corradini, A., Ossi, F. & Cagnacci, F. Bridging human mobility to animal activity: when humans are away, bears will play. in *Proceedings of the 2nd ACM SIGSPATIAL International Workshop on Animal Movement Ecology and Human Mobility* 1–8 (ACM, Seattle, Washington, 2022). https://doi.org/10.1145/3557921.3565538
24. Dewey. Academic Research Data. https://www.deweydata.io. Accessed: 17 March 2025.
25. Advan Research. Location and Sales Data For Finance, Retail & Commercial Real Estate. https://advanresearch.com. Accessed: 17 March 2025.

26. Feng, A. et al. Transmission of SARS-CoV-2 in free-ranging white-tailed deer in the United States. *Nat. Commun.* **14**, 4078 (2023).
27. U.S. Census Bureau. Urban and Rural. https://www.census.gov/programs-surveys/geography/guidance/geo-areas/urban-rural.html. Accessed: 17 March 2025.
28. Esri Inc. Light Gray Canvas. https://www.arcgis.com/home/item.html?id=979c6cc89af9449cbeb5342a439c6a76. Accessed: 16 May 2025.
29. Roden-Reynolds, P., Kent, C. M., Li, A. Y. & Mullinax, J. M. Patterns of white-tailed deer movements in suburban Maryland: Implications for zoonotic disease mitigation. *Urban Ecosyst.* **25**, 1925–1938 (2022).
30. Abernathy, H. N. et al. Dynamic riskscapes for prey: disentangling the impact of human and cougar presence on deer behavior using GPS smartphone locations. *Ecography* e07626 (2025).
31. Veraset. Global mobility and location data provider. https://www.veraset.com/. Accessed: 17 March 2025.
32. National Household Travel Survey. https://nhts.ornl.gov. Accessed: 17 March 2025.
33. Howard County Maryland. Parks. Howard County Maryland Data Download and Viewer. https://data.howardcountymd.gov/. Accessed: 10 October 2024.
34. Bondarenko, M., Kerr, D., Sorichetta, A. & Tatem, A. *Census/projection-disaggregated gridded population datasets for 189 countries in 2020 using Built-Settlement Growth Model (BSGM) outputs.* WorldPop (University of Southampton, UK, 2020). https://doi.org/10.5258/SOTON/WP00684
35. U.S. Census Bureau. Decennial Census of Population and Housing by Decades. https://www.census.gov/programs-surveys/decennial-census/decade.html. Accessed: 17 March 2025.
36. Wan, Z., Hook, S. & Hulley, G. MODIS/Terra land surface temperature/emissivity 8-Day L3 global 1km SIN grid V061. NASA EOSDIS Land Processes Distributed Active Archive Center. https://doi.org/10.5067/MODIS/MOD11A2.061 (2021).
37. Robinson, C. et al. Large scale high-resolution land cover mapping with multi-resolution data. in *Proceedings of the Conference on Computer Vision and Pattern Recognition (CVPR 2019)* (CVPR, 2019).
38. Pebesma, E. Simple features for R: standardized support for spatial vector data. *R. J.* **10**, 439 (2018).
39. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (2024).
40. McGarigal, K., Cushman, S., Ene, E. & FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors. https://www.fragstats.org (2023). Accessed: 23 January 2025.
41. LaGro, J. Assessing patch shape in landscape mosaics. *Photogram. Eng. Remote Sens.* **57**, 285–293 (1991).
42. Hesselbarth, M. H. K., Sciaini, M., With, K. A., Wiegand, K. & Nowosad, J. *landscapemetrics*: an open-source *R* tool to calculate landscape metrics. *Ecography* **42**, 1648–1657 (2019).
43. Howard County Maryland. Buildings_Major. Howard County Maryland Data Download and Viewer. https://data.howardcountymd.gov/. Accessed: 30 May 2024.
44. Howard County Maryland. Land Use. Howard County Maryland Data Download and Viewer. https://data.howardcountymd.gov/. Accessed: 30 May 2024.
45. U.S. Census Bureau. 2023 TIGER/Line Shapefiles. https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.2023.html#list-tab-790442341 (2023).
46. Oyeyemi, G. M., Ogunjobi, E. O. & Folorunsho, A. I. On performance of shrinkage methods—A Monte Carlo study. *Int. J. Stat. Appl.* **5**, 72–76 (2015).
47. NIMBLE Development Team. NIMBLE: MCMC, particle filtering, and programmable hierarchical modeling. Zenodo https://doi.org/10.5281/ZENODO.1211190 (2024).
48. Gelman, A. & Rubin, D. B. Inference from iterative simulation using multiple sequences. *Stat. Sci.* **7**, 457–472 (1992).

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Author contributions

S.A.P., T.G., J.M., A.R., G.P.M., and T.A. conceptualized the study. J.M. and T.A. provided the data. S.A.P. and T.G. performed the analysis. S.A.P., T.G., J.M., A.R., and T.A. interpreted the results. S.A.P., T.G., and T.A. wrote the manuscript. All authors reviewed the manuscript. T.G., J.M., A.R., and T.A. secured funding related to this research.

Declarations

Competing interests

The authors declare no competing interests.

Ethics approval

The deer trapping protocol was approved by the Animal Care and Use Committee (IACUC approval #16–024) of the United States Department of Agriculture Beltsville Agricultural Research Center. All methods were carried out in accordance with relevant guidelines and regulations.

Additional information

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