MOVEMENT ECOLOGY

Interacting effects of human presence and landscape modification on birds and mammals

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Sustainable human–wildlife coexistence requires a mechanistic understanding of the many ways that humans affect animals. However, progress is hampered by the lack of accessible data measuring the dynamic presence of people. Here, we leverage mobile-device data to disentangle how human presence and landscape modification differentially influence the use of geographic and environmental space for 37 mammal and bird species across the United States. Human presence affected more than 65% of species, with substantial variation across species. For ~60% of species that responded to human activities, the effects were interdependent—animals tended to react more strongly to human presence in less modified habitats. Our results demonstrate that human presence and landscape modification have complex combined effects on wildlife, which need to be considered for effective management.

Human activities are driving catastrophic loss of biodiversity around the world by altering the climate and reshaping land- and seascapes (*1*–*3*). As the march of human encroachment continues, a mechanistic understanding of how humans and wildlife may coexist is critical to maintaining biodiversity (*4*). Doing so requires charting the many interacting ways in which human activities influence wildlife. Typically, the intensity of landscape modification through urbanization, agriculture, transportation, and energy infrastructure is assumed to be a robust proxy of human impacts [e.g., (*5*–*8*)]. However, a rich theoretical literature predicts that the physical presence of humans themselves can also substantially affect how animals perceive risk, with major consequences for their use of space and resources and interactions with other species (*9*–*11*).

The dynamic presence of humans and their vehicles is rarely considered in ecological studies, presumably because data at sufficiently fine spatial and temporal scales are largely inaccessible (*12*). Therefore, whether human presence is a major driver of wildlife behavior has only been directly tested in local settings, where data on humans and wildlife can sometimes be collected in tandem, or at regional scales using coarse proxies of human presence, such as pandemic-related lockdowns [e.g., (*13*–*15*)]. Moreover, recent research has primarily focused on mammals, with little work investigating the effects of human presence on other taxonomic groups. Finally, whether multiple forms of human activities have additive or interacting influences on wildlife has not been well established (*16*, *17*). Failing to explicitly quantify the presence of humans as an independent driver may obfuscate the ways in which humans affect animal behavior, physiology, demography, and ultimately population viability (*18*, *19*).

We investigated how two major components of human activity—human presence and landscape modification—affect the use of geographic and environmental space by mammals and birds across the continental United States of America (US) (Fig. 1A). We focused our study during the years 2019 and 2020, to leverage high-resolution human-mobility data, which measure daily human presence, that had been temporarily available to researchers during the COVID-19 pandemic (*20*, *21*). The policies to restrict human movement during the early pandemic period also disrupted the typical positive association between human presence and landscape modification, thus decoupling the usually confounded effects of these drivers (*22*–*25*).

Animals' use of geographic and environmental space reflects an optimized trade-off between energy expenditure and acquisition and may vary on the basis of species' traits and life-history strategies (*26*, *27*). Human activities may cause animals to use more area as they take less direct routes to avoid contact or explore alternative habitats (*28*, *29*). Alternatively, modifications to landscapes can render them impermeable to wildlife (*8*, *15*, *30*), constraining the amount of area available for use, or animals may cover less area as they exploit concentrated resource pockets of anthropogenic food sources (*31*). Changes in the size of animals' environmental niches indicate a shift in the resources or habitats used, or more generally, a change in exposure to environmental conditions (*32*, *33*). Therefore, human activities may narrow animals' environmental niches by constraining the habitats they can access or broaden their niches by disrupting access to preferred habitats and necessitating the use of marginal ones. Alternatively, human activities could change niche size without a corresponding change in area size by altering the locations individuals used, indicating that species either switched to alternative habitats or were pushed into suboptimal ones, but these alternative explanations cannot be distinguished without information on individuals' fitness. Because human presence and landscape modification can affect wildlife through multiple mechanisms that depend on species' real and perceived risk, we predicted that responses to each component would vary strongly by species and environmental context.

We estimated the daily presence of humans, normalized by area, using mobile-device counts (SafeGraph; safegraph.com) available at the US Census block group level and landscape modification based on a multiyear aggregated metric of anthropogenic modification within 1 km^2 pixels (Fig. 1A and fig. S5) (*34*). We used locations recorded by animal-mounted GPS devices to derive two metrics for each individual on a weekly basis from January through August, inclusive, of both years (Fig. 1A and table S1). First, we used dynamic Brownian bridge movement models to estimate the amount of geographic space used by individual animals on a weekly basis (hereafter "area size"; figs. S1

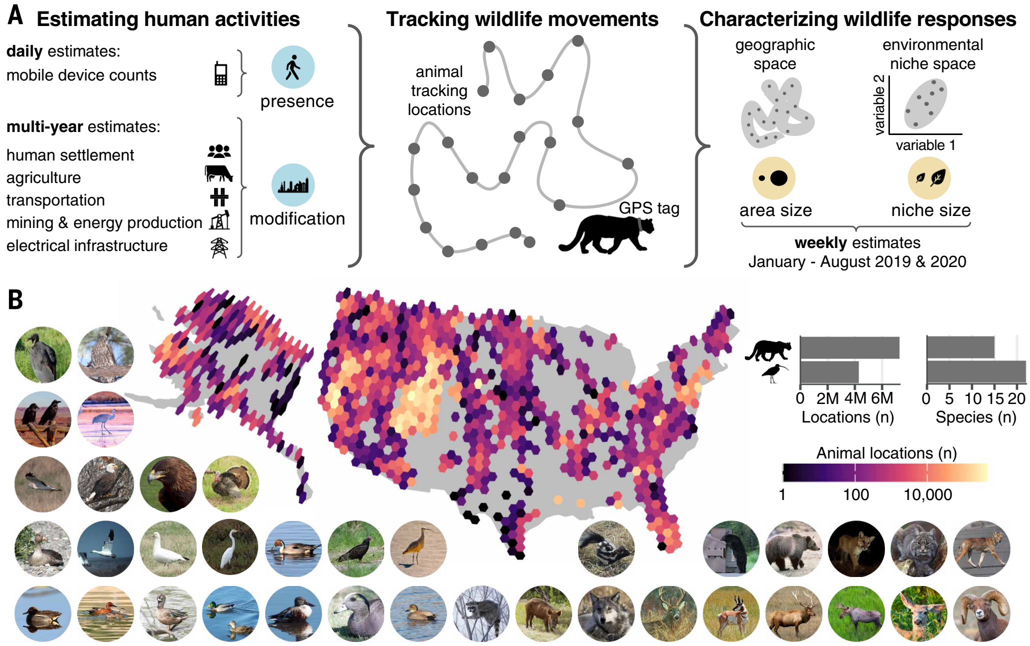

Fig. 1. Wildlife responses to the major components of human activity across the United States. (**A**) The impact of human activities was quantified by linking daily estimates of human presence and multiyear estimates of landscape modification, respectively, to locations of GPS-tagged animals. GPS locations were used to estimate animals' weekly area and niche size (*36*). (**B**) Responses were examined for 37 bird and mammal species across the continental United States, based on ~11.8 million animal locations from 4581 individuals. [Image credits: Plains spotted skunk, Clint Perkins; Great egret, Nils Warnock; all other images, Creative Commons Zero (CC0) or public domain (supplementary text)]

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and S6 and table S3) (*35*, *36*). Second, we estimated the weekly environmental niche size of individual animals, defined as the pooled variance of multidimensional hypervolumes of the set of environmental conditions across recorded GPS locations (hereafter "niche size"; fig. S2) (*36*, *37*). We estimated responses of area and niche size to human presence and landscape modification for birds ($n = 22$ species) and mammals ($n = 15$ species) based on ~11.8 million animal-tracking locations (n = 4581 individuals) using species-specific Bayesian generalized linear mixed effects models. All models controlled for environmental conditions (i.e., vegetation productivity and air temperature) and for area size in niche size models (Fig. 1B and table S2) (*36*).

Interacting effects of human activities

Human presence was associated with changes in area or niche size for 67% of the mammal species and 68% of the bird species studied (Fig. 2A). More than half of species (57%) were affected by both human presence and landscape modification (Fig. 2B; area size: 46%; niche size: 27%). For most species (59%) that responded to human activity, the effects of human presence and landscape modification on area or niche size were interactive (i.e., the response to one driver depended on the strength of the other) (Fig. 2A). Altogether, our findings show that species responded to human presence and landscape modification by changing the amount of area used, adjusting the size of their environmental niches, or both (Fig. 2C). These results demonstrate that directly quantifying the presence of humans over short timescales is necessary to fully capture the impact of human activity on wildlife.

Most mammal species (67%) contracted the amount of area used in response to human presence or landscape modification (Fig. 2A). Many (40%) mammal species that responded to human presence reacted more strongly in less modified habitats, suggesting that some populations inhabiting more developed areas are either habituated to humans or cannot further reduce the amount of area they use while also maintaining access to critical resources (*17*). Gray wolves (*Canis lupus*) are an exception and expanded the amount of area they used in response to both human presence and landscape modification. Gray wolves have faced considerable persecution throughout North America and are considered to be particularly sensitive to humans (*38*). Their expanded use of space could reflect a requirement to cover more area to avoid human activities (*28*, *29*).

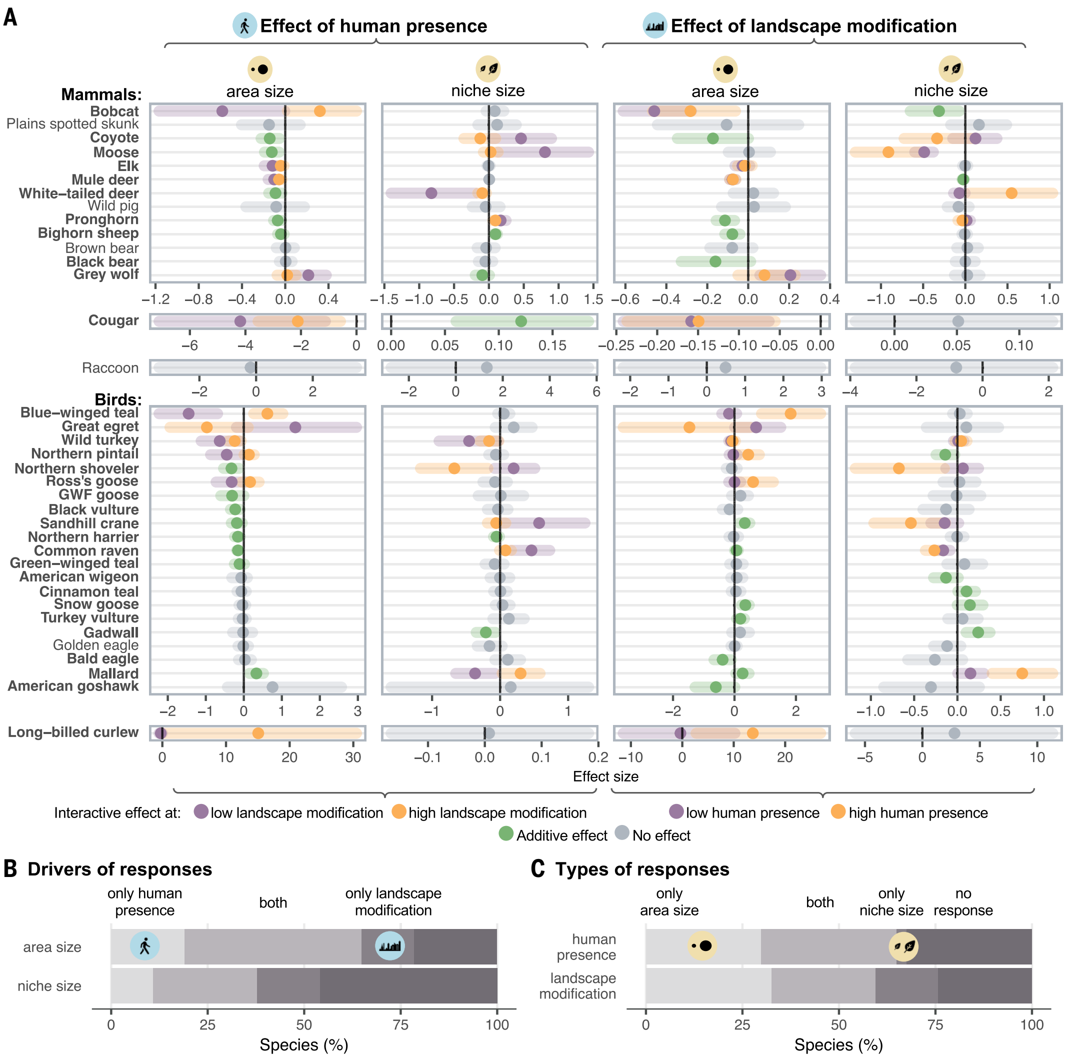

Fig. 2. Interacting effects of human activities on wildlife's use of geographic and environmental space. (**A**) Effects of human presence and landscape modification on area and niche size used by animals on a weekly timescale. Points show effect-size estimates with 95% credible intervals. Species names in bold indicate species with at least one significant response. Full model results and sample sizes can be found in table S2 and figs. S7 to S80. Effect sizes for cougars, raccoons, and long-billed curlews are shown separately, on different scales. (**B**) The majority of species responded to both human presence and landscape modification. (**C**) Species responded to human presence and landscape modification by changing their area size, niche size, or both.

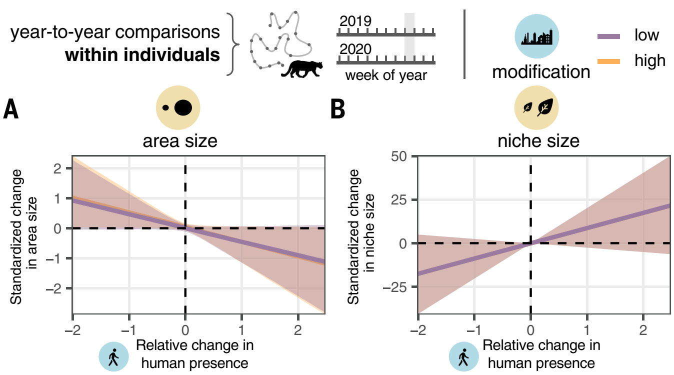

Fig. 3. Plastic behavioral responses to human presence. Conditional effects of changes in human presence on the changes in (**A**) area and (**B**) niche size for individual animals on a weekly basis compared between 2019 and 2020. Shading indicates 95% credible intervals. The credible intervals for high- and low-modification estimates are overlapping because of a lack of a significant global interactive effect. Sample size: n = 19,453 individual-week pairs, 1251 individuals, 13 species.

The presence of humans also contracted the amount of area used by 41% of the bird species studied (Fig. 2A). For many of these species, the magnitude and direction of the effect of human presence depended on the degree of landscape modification. For example, human activities restricted the amount of area used by wild turkeys (*Meleagris gallopavo*), but they responded less strongly to human presence in more modified environments. By contrast, the direction of the response to human presence for great egrets (*Ardea alba*) depended on the degree of landscape modification. Species that rely on patchily distributed habitats may be less likely to switch patches in highly developed environments, whereas dispersal may be more likely in relatively undeveloped contexts (*39*).

When controlling for weekly area size in niche size models (*36*), we found that, for many species, human presence and landscape modification had opposing effects on environmental niches (Fig. 2A). However, the direction of responses varied across species for both birds and mammals. For example, human presence and landscape modification had opposing effects on the niche sizes of white-tailed deer (*Odocoileus virginianus*) and sandhill cranes (*Grus canadensis*), albeit with different directions of responses. White-tailed deer, a highly human-affiliated species in the US, expanded their environmental niches with increasing landscape modification but contracted their niches with increasing human presence (*40*). Sandhill cranes, a non–human-affiliated species, showed the opposite response. These responses may reflect divergent responses to humans where synanthropic species integrate modified environments into their environmental niches, whereas less habituated species rely on increasingly isolated patches of habitat.

Behavioral plasticity to changes in human presence

To test whether species-level responses were driven by behavioral plasticity of individual animals to year-to-year differences in human activities or differential responses among individuals within species, we used locations from individual animals that were tracked in both 2019 and 2020. Using Bayesian mixed effects models to control for environmental conditions and sampling design, we compared weekly year-to-year differences to estimate the impact of relative changes in human presence on area and niche size of individual animals (*36*).

As with our species-level analysis, we found that year-to-year differences in human presence were generally negatively associated with changes in area size and positively associated with changes in niche size for individual animals, although species-specific responses varied (Fig. 3 and fig. S3; area size marginal effect at median landscape modification: $\beta = -0.48$, 95% credible interval (CI) = [−1.37, 0.08], Bayesian probability of direction (pd) = 96.0%; niche size marginal effect at median landscape modification: $\beta = 13.03$, 95% CI = [8.84, 32.88], pd = 90.7%). Because we observed that individual animals responded to changes in human activities, these results provide evidence that the observed species-level responses are at least partially driven by the behavioral plasticity of individual animals as opposed to differential responses among individuals. We found little support for a global interactive effect between changes in human presence and landscape modification in either area size ($\beta = -0.08$, 95% CI = [−0.41, 0.22], pd = 74.5%) or niche size ($\beta = 0.05$, 95% CI = [−0.45, 0.34], pd = 65.4%). However, as with the main effect of human presence, species varied in their responses, with some showing an interactive effect between human presence and landscape modification (fig. S4). As with our species-level analysis, these results suggest that the interacting effects of human presence and landscape modification are not consistent across species.

Combined impact of human activities on wildlife

To estimate the combined impact of human presence and landscape modification on wildlife area and niche sizes, we compared predicted area and niche sizes at low and high levels of human activity for species that showed significant responses to human activity (20% and 80% species-specific quantiles of observed human presence and landscape modification). We restricted predictions to species that showed significant responses because predictions for species without responses would not differ under low and high levels of human activity.

Of species with significant responses to human activities, mammals reduced the amount of area that they used on a weekly basis by a median of 11% per animal (range = [−35.9, 15.7 km^2]) and birds exhibited a median decrease of 1.8% per animal (range = [−171.4, 72.6 km^2]) (Fig. 4). However, there was substantial variation among species. For example, we estimated that human activities caused coyotes (*Canis latrans*) to use 11.3 km^2 less area per week per animal, whereas common ravens (*Corvus corax*) used 26 km^2 more area per week per animal. These seemingly alternate responses may be driven by the same mechanism, as both coyotes and ravens are known to exploit anthropogenic food sources (*28*, *41*, *42*). However, coyotes face substantial persecution by humans and therefore may do so by restricting their territories, whereas ravens may be emboldened to cover larger areas to access anthropogenic subsidies.

We also found that the impact of human activity contracted species' environmental niches by a median of 2.8%, although there appeared to be substantial interspecific variation (mammals: median = −7.7%, range = [−58.3%, 40.15%]; birds: median = −2.2%, range = [−63.5%, 62.1%]). For example, we estimated that human activities caused common ravens to narrow their environmental niche by 46%, whereas cougars (*Puma concolor*) broadened theirs by 10%. These results suggest that ongoing human activities have substantial effects on how animals interact with their environment. However, more detailed information on the form of human activities would be needed to precisely define the impact of these effects.

Concluding remarks

Our work demonstrates that for many species, the effects of landscape modification cannot be understood without taking into account the presence of humans, which can both amplify and dampen its effects. These results indicate that human presence must be explicitly considered to appropriately assess anthropogenic impacts on wildlife. Notably, we were unable to interpret whether observed responses represented a cost or subsidy to animals without more detailed information on the nature of human activities (e.g., hiking versus hunting, presence of anthropogenic food) or the fitness consequences of the observed effects. However, the current access model for human-mobility data necessary to explore these nuances largely prevents their use in conservation research (*43*). Further, the spatial resolution of many human-mobility datasets does not capture the fine-scale behavioral responses necessary to support human–wildlife coexistence.

The identification of multiple types of responses across species suggests that there are distinct pathways by which wildlife species respond

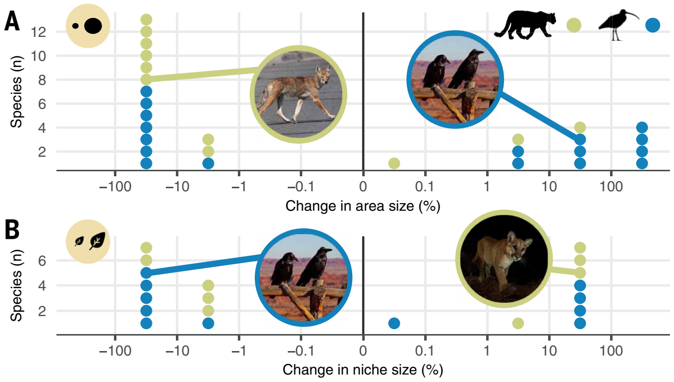

Fig. 4. Combined impact of human activities on wildlife use of geographic and environmental space. Predicted changes in (**A**) area and (**B**) niche size based on the difference between high– and low–human activity scenarios for species that showed significant responses to human activity. Points represent the median predicted change in area and niche sizes for an individual animal for each species. Human activity scenarios were estimated on the basis of species-specific 20% (low) and 80% (high) quantiles of observed human presence and landscape modification. Percent change is shown on the logarithmic scale. Species without significant responses are not shown (area size: $n = 22$; niche size: $n = 14$). All images are CC0 or public domain (supplementary text).

to human activities, which could help inform species-specific management. Future work should test the consistency and generality of these pathways across a greater range of taxa as well as how response types relate to population demography (*44*, *45*). The varied responses that we observed across species reflect substantial differences in species' ecology and environmental context, as well as affiliations with humans. Our study was necessarily restricted to species that can be tracked with GPS devices, which excludes most smaller-bodied birds and mammals, which may respond differently to human activities.

Although climate change and habitat loss will continue to place extreme pressure on wildlife populations (*46*), our results indicate that progress toward human–wildlife coexistence may be achieved through recognizing, and mitigating, the distinct effect of human presence. Conservation benefits could be realized, for example, through the dynamic regulation of human use of wild areas throughout the day and year, as opposed to strict exclusion. For example, it may be possible to manage temporal patterns of vehicular traffic to minimize impacts on wildlife during critical periods or in important environmental refugia (*47*–*49*). Global coordination is undoubtedly needed to tackle the biodiversity crisis, but our study has highlighted that there is scope for rapid, local action, using nuanced policies to manage human–wildlife interactions.

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R.Y.O., S.W.Y., and C.R. hold advisory roles with or participate in MoveBON. The authors declare no other competing interests. **Data, code, and materials availability:** All data, including environmental annotations, area-normalized human mobility data, and estimated area and niche size as well as code to reproduce results are available on the Open Science Framework (*50*). Animal tracking datasets are available on Movebank Repository, DataDryad, or USGS Science Base through individual data publications (*51*–*83*). A subset of animal tracking datasets are not publicly available because of conservation concern but will be made available for research purposes on request (see table S1 for contact information for each dataset). Human modification data are publicly available on Figshare (*84*).

SUPPLEMENTARY MATERIALS

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Materials and Methods; Supplementary Text; Figs. S1 to S80; Tables S1 to S3; References (*85*–*122*); Reproducibility Checklist

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Interacting effects of human presence and landscape modification on birds and mammals

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Editor's summary

Agriculture, settlements, roads, and other infrastructure profoundly shape the habitats that are available to nonhuman animals. In addition to changing their behavior to avoid or exploit these new hazards and resources, many species may also directly avoid humans. Oliver *et al*. examined how bird and mammal habitat use depends on both human land use and direct human presence using mobile device data to determine where people are (see the Perspective by Beaudrot). Across 37 species with geolocation data in the United States, most species responded directly to human movements, with most of these showing interactive effects between human land use and human presence. Considering only human effects on land cover will thus often provide inaccurate assessments of species' habitat use.
—Bianca Lopez

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