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Wherever I may roam—Human activity alters movements of red deer (*Cervus elaphus*) and elk (*Cervus canadensis*) across two continents

Steffen Mumme[1,2,3] | Arthur D. Middleton[3] | Paolo Ciucci[1] | Johannes De Groeve[2,5] | Andrea Corradini[2,4,6,7] | Ellen O. Aikens[8,9] | Federico Ossi[2,4] | Paul Atwood[10] | Niko Balkenhol[11] | Eric K. Cole[12] | Lucie Debeffe[13,14,†] | Sarah R. Dewey[15] | Claude Fischer[16] | Justin Gude[17] | Marco Heurich[18,19,20] | Mark A. Hurley[21] | Anders Jarnemo[22] | Matthew J. Kauffman[23] | Alain Licoppe[24] | Emiel van Loon[5] | Doug McWhirter[25] | Tony W. Mong[26] | Luca Pedrotti[7] | Nicolas Morellet[13,14] | Atle Mysterud[27] | Wibke Peters[28] | Kelly Proffitt[29] | Sonia Saïd[30] | Johannes Signer[11] | Peter Sunde[31] | Martin Starý[32] | Francesca Cagnacci[2,4]

Correspondence
Steffen Mumme, Department of Zoology and Physiology, University of Wyoming, Laramie, WY, USA.
Email: mumme.steffen@gmail.com

Abstract

Human activity and associated landscape modifications alter the movements of animals with consequences for populations and ecosystems worldwide. Species performing long-distance movements are thought to be particularly sensitive to human impact. Despite the increasing anthropogenic pressure, it remains challenging to understand and predict animals' responses to human activity. Here we address this knowledge gap using 1206 Global Positioning System movement trajectories of 815 individuals from 14 red deer (*Cervus elaphus*) and 14 elk (*Cervus canadensis*) populations spanning wide environmental gradients, namely the latitudinal range from the Alps to Scandinavia in Europe, and the Greater Yellowstone Ecosystem in North America. We measured individual-level movements relative to the environmental context, or movement expression, using the standardized metric Intensity of Use, reflecting both the directionality and extent of movements. We expected movement expression to be affected by resource (Normalized Difference Vegetation Index, NDVI) predictability and topography, but those factors to be superseded by human impact. Red deer and elk movement expression varied along a continuum, from highly segmented trajectories over relatively small areas (high intensity of use), to directed transitions through restricted corridors

Arthur D. Middleton, Paolo Ciucci and Francesca Cagnacci co-advised the study.

†Deceased. Lucie left us suddenly, leaving a great void among us. We all miss her cheerfulness, her enthusiasm, and her ever-present smile in everyday life and in her research work. Her endless support, experience, and knowledge helped to shape this manuscript, she unfortunately left us before this work saw the light of day.

(low intensity of use). Human activity (Human Footprint Index, HFI) was the strongest driver of movement expression, with a steep increase in Intensity of Use as HFI increased, but only until a threshold was reached. After exceeding this level of impact, the Intensity of Use remained unchanged. These results indicate the overall sensitivity of *Cervus* movement expression to human activity and suggest a limitation of plastic responses under high human pressure, despite the species also occurring in human-dominated landscapes. Our work represents the first comparison of metric-based movement expression across widely distributed populations of a deer genus, contributing to the understanding and prediction of animals' responses to human activity.

KEYWORDS

Anthropocene, *Cervus* spp., human footprint, migratory ungulates, movement expression, wildlife

1 | INTRODUCTION

Movement is an essential element of an animal's life, shaped by internal processes and the environment to ensure reproduction and survival (Nathan et al., 2008). The spatiotemporal availability and predictability of trophic resources, in particular, is one major environmental driver shaping animal movements across heterogeneous landscapes (Armstrong et al., 2016). In large herbivores, different movement patterns can emerge under specific environmental conditions (Eggeman et al., 2016): the timing and extent of seasonal migratory movements (Peters et al., 2019; Rickbeil et al., 2019), recurring displacements between portions of the ranges (e.g., commuting tactics, Cagnacci et al., 2016, Couriot et al., 2018), or consistency of yearly trajectories (Morrison et al., 2021), may strongly vary both within and across ungulate populations. For example, seasonal migration and year-round residency may coexist within the same population, resulting in partial migration (roe deer *Capreolus capreolus*: Cagnacci et al., 2011; red deer *Cervus elaphus*: Mysterud et al., 2011). In addition, in species such as red deer and elk (*Cervus canadensis*), the tendency to migrate can change within the lifetime of an individual, referred to as facultative migration (Eggeman et al., 2016). In essence, movements of ungulate species can be described as a *continuum* of tactics adopted in specific environmental contexts (Martin et al., 2018), or "movement expression," which is the observable outcome of ecological plasticity. The drivers causing the emergence of such a continuum have thus far proven to be challenging to disentangle, especially as anthropogenic influence on ecosystems becomes more prevalent. Here, we propose to quantify movement expression using individual-level movement metrics and study the key factors that influence its variation within and between populations. We take advantage of analyzing movement of two species of the same genus (*Cervus* spp.—red deer and elk; Hu et al., 2019) that evolved in biogeographic continuity, with very similar anatomical structure, movement capacity, and navigation abilities (sensu Nathan et al., 2008), but located in very diverse environmental contexts across continents. This way, we could assess the effect of anthropogenic impact and spatiotemporal predictability of resources on movement expression across a very broad environmental gradient.

Several studies provided evidence of broad-scale impacts of human activity on animal movement, such as shortened displacements, alternated movement rates and timing, and decreased home range sizes (Doherty et al., 2021; Main et al., 2020; Tucker et al., 2018; Wyckoff et al., 2018). For ungulates, anthropogenic infrastructure such as roads, railways, and fences are well known to act as barriers (Benítez-López et al., 2010; Linnell et al., 2016; McInturff et al., 2020). The presence of infrastructure can disrupt both long-distance movements, such as in Mongolian gazelles (*Procapra gutturosa*; Nandintsetseg et al., 2019), Asiatic wild asses (*Equus hemionus kulan*; Ito et al., 2013), and mule deer (*Odocoileus hemionus*; Wyckoff et al., 2018), and short-distance movements, such as in elk (Prokopenko et al., 2017) and roe deer (Passoni et al., 2021). A resulting major threat of infrastructure for ungulate movement behavior is the decrease in connectivity between suitable habitat patches (Fahrig, 2007; Tucker et al., 2018). Loss of connectivity may yield habitat fragments too far away to be encompassed in single home ranges or separated by barriers so that foraging opportunities can be altered. Furthermore, movements between remaining fragments through non-suitable habitats can result in increased mortality risk, for example due to predator encounter (Zimmermann et al., 2014; see also Cagnacci, 2023) or wildlife–vehicle collisions (Morelle et al., 2013). Red deer have been shown to adapt their temporal space-use patterns when exposed to roads, such as using areas in proximity during times of low traffic (Meisingset et al., 2013) or by avoiding roads in general (D'Amico et al., 2016). In contrast, some types of human activities can be attractive for ungulate populations, such as irrigated agriculture fields, which can locally increase resource availability and provide nutritional benefits for individuals using those areas (Middleton et al., 2013). Also in such cases, human impact may lead to changes in movement patterns; for example, artificial forage subsidies may favor residence over migration in landscapes otherwise characterized by natural resource heterogeneity that would typically induce migration (Barker et al., 2019; Middleton et al., 2013).

We used data from 28 populations, of which 14 in the Greater Yellowstone Ecosystem (GYE) in western North America and 14 in European landscapes (Euromammals; Urbano et al., 2021). The populations were specifically chosen to sample movement expression across landscapes strongly differing in levels of human activity. The diversity in population contexts, ranging from wilderness areas under full protection in the GYE to populations roaming in semi-urban environments in European landscapes, allowed us to test the effect of a steep gradient of human activity on red deer and elk movement expression at a large spatial scale. We assessed the movement expression at the individual level using the standardized metric Intensity of Use, summarizing the linear and area-based extent of movement (the rate between the path length and the square root of the area covered; Almeida et al., 2010).

Because movement is the result of the interaction between an animal's internal state and the external context they experience (Nathan et al., 2008) and because both red deer and elk show a high degree of ecological plasticity (Peters et al., 2017; Rickbeil et al., 2019) and have a very similar anatomical structure, movement capacity, and navigational abilities, we hypothesized that individual movement expression would be affected more by the landscape-scale environmental drivers than by continental or species differences (Hypothesis 1; Prediction 1.1). We further assessed how different drivers at the landscape scale would affect movement expression. Specifically, we hypothesized that even though the topography and forage resource predictability of the landscapes will have a role in shaping red deer and elk movements, such effects would be outweighed by human activity (Hypothesis 2). As landscapes with pronounced topography are linked to high habitat heterogeneity and environmental gradients can trigger long-distance movements in ungulates (Peters et al., 2019; Teitelbaum et al., 2015), we predicted that individual movements would be highly directional along these gradients, characterized by lower Intensity of Use values (Prediction 2.1). Furthermore, because red deer and elk have been shown to synchronize their movements to predictable vegetation green-up patterns (Aikens et al., 2020; Merkle et al., 2016; Mueller et al., 2011), we predicted that in environments with highly predictable resources, animals would perform more directional movements (i.e., characterized by lower Intensity of Use values, such as migration) to exploit fleeting seasonal resources (Prediction 2.2). Conversely, we predicted that red deer and elk would respond to anthropogenic barriers and fragmentation with truncated and more tortuous movements carved across the anthropogenic matrix (i.e., higher Intensity of Use as Human Footprint Index [HFI] increases; Prediction 2.3). On top, because animals need to gain enough resources to survive and reproduce, we predicted that animals' possibility to adjust their movements to anthropogenic landscapes would be limited beyond a certain level of human activity (Prediction 2.4a; i.e., Intensity of Use leveling to a maximum value beyond a threshold value of human activity); as an alternative prediction, in areas with high human activity red deer and elk might be forced to express more directional movements to cross barriers to access enough suitable habitat patches to support their lives (Prediction 2.4b; i.e., Intensity of Use dropping beyond a threshold value of human activity).

2 | MATERIALS AND METHODS

2.1 | Animal movement data set

We compared movement expressions of red deer and elk across a wide geographic range that covered a diversity of environmental contexts (Figure 1). For the European populations, the data were provided through Eureddeer, the red deer data collaboration project as part of Euromammals (http://euromammals.org/; Urbano et al., 2021). The North American data sets were provided by the Wyoming Game and Fish Department, University of California Berkeley, University of Wyoming, National Park Service, US Fish and Wildlife Service, Montana Fish, Wildlife and Parks, and Idaho Fish and Game (Appendix S1: Table S1-1 and Figure S1-1). Because we focus on movement expression during times of seasonal movement potentially including long-distance migrations, that typically occur in spring and fall (see reference dates in Peters et al., 2019, for Europe, and Rickbeil et al., 2019, for North America), winter data were not included in the data set, and therefore all trajectories were subsampled to the study period between the 1 April and the 30 November (Appendix S2). To enhance data availability and decrease noise, Global Positioning System (GPS) trajectories were subsampled to a 2-day resolution and missing locations (2.4% of the data set) were interpolated (linear interpolation method, R package *adehabitatLT*, Calenge, 2006). When data gaps exceeded 8 days, the trajectory was discarded from the analysis. The regularized trajectories were checked visually and numerically for errors and artifacts, and when needed, they were cleaned using standard methods (Appendix S2). The resulting data set included 815 GPS-tracked individuals belonging to 28 populations, spanning 1206 animal-years from 1999 to 2019 (Table S1-1).

2.2 | Environmental variables

To characterize the environmental and anthropogenic context, animals were exposed to at the landscape scale and relate these external drivers to their movement, we extracted three different variables across population ranges: predictability of vegetation phenology, topography, and human activity. All variables were sampled at the GPS location level within the sampling period (April–November) and averaged at the individual trajectory level (i.e., animal-year trajectory). This way, we evaluated the effect of animals' *exposure* to environmental variables ("use," sensu Manly et al., 2002) on the resulting movement (see also the movement ecology paradigm, Nathan et al., 2008: external state as a determinant of individual patterns of movement). For the statistical analysis and prior to model development, all environmental variables were scaled and standardized (hereafter: scaled values) by subtracting the mean and dividing by the standard deviation, to assure comparable effect sizes. For visualization purposes, we then plotted the environmental variables on the original scale.

We used the Normalized Difference Vegetation Index (NDVI), which measures vegetation vitality using the near infrared and red light
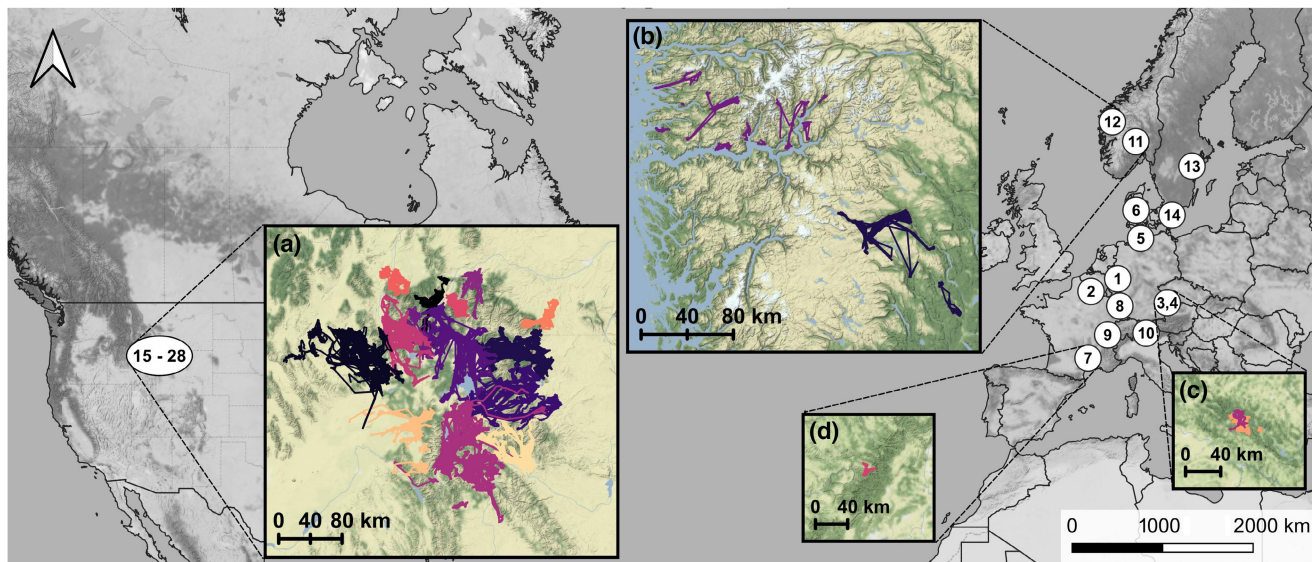
FIGURE 1 Map of the studied red deer and elk populations across Europe and Western North America. In Europe, populations (1–14) span from Scandinavia to southern France, covering an altitudinal gradient from about 200 to 2500 m a.s.l. The North American populations (15–28) are situated in the Greater Yellowstone Ecosystem, which encloses Yellowstone National Park in its core, and are distributed over the three states of Wyoming, Montana, and Idaho. All magnification panels (in color) are set to the same scale (equidistant) and show largely migratory populations in the GYE (a) and Norway (b) and populations with shorter migration distances in Bavarian National Park in Germany, Sumava National Park in Czech Republic (c) and Cévennes National Park in southern France on the edge of the Massif Central (d). The base map features hill shades and natural vegetation colors ("Stamen Terrain," Stamen Design 2021). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

spectrums of remotely sensed satellite imagery (Vuolo et al., 2012; here MODIS imagery at a spatial resolution of 250m), to specifically assess the predictability of vegetation phenology (NDVI predictability) across population ranges. We calculated NDVI predictability using equations from Colwell (1974) and applying them to the NDVI time-series data in the *hydrostats* R package (Bond, 2019). With this index, we assessed the overall spatiotemporal predictability of productivity across different environmental contexts (English et al., 2012). We used NDVI predictability in this study as more context-specific green-up and vegetation senescence dynamics are expected to be highly variable across the studied populations (for details and applications, see Bond, 2019; Peters et al., 2017, and Appendix S3).

Topographic landscape information was extracted from digital elevation models (DEMs) available through Copernicus for Europe (EU-DEM version 1.1, European Environment Agency [EEA], 2020) and the Shuttle Radar Topography Mission (STRM; USGS, Koch & Heipke, 2001) for the North American study areas, with 25- and 30-m spatial resolution, respectively. We characterized the topography of the study area by deriving elevation, slope, and terrain roughness from each cell of the available DEMs across all studied populations.

The level of human activity was estimated using the multi-proxy HFI available at a spatial resolution of 1 km^2 (HFI, Venter et al., 2018, downloaded from the NASA/SEDAC website). The Index measures the anthropogenic pressure put on nature, with values ranging from 0 (untouched by human activity) to 50 (maximum human impact; Venter et al., 2016, and further details in Appendix S3). High levels

of the HFI can encompass both anthropogenic impediments to animal movement, such as human encroachment or infrastructure, or attractants, such as seasonal resource provision associated with irrigated agriculture. To clarify this ambiguity, we refer to all impacts considered by the HFI as human activity in this work.

2.3 | Movement metric 'Intensity of Use'

We characterized the movement expression of individuals across different environmental contexts and populations by computing the movement metric Intensity of Use (Almeida et al., 2010) at the individual trajectory level (i.e., animal-year). This metric:

$$\text{Intensity of use } I = \frac{L}{\sqrt{A}} \text{ with } \{I \in R \mid I \geq 0\},$$

calculates the ratio between the total distance traveled (i.e., path length) and the square root of the corresponding area the animals have moved through (Minimum Convex Polygon defined by the trajectory), providing an area-standardized measure of the directionality of movements. We selected Intensity of Use after performing an exploratory cluster analysis to visualize how populations would be grouped based on the mean and standard deviation of Intensity of Use and two other simpler population-level movement metrics (total distance traveled and maximum linear distance covered; see Appendix S4: Table S4-1 and Figure S4-2). The classification based

on Intensity of Use was mostly consistent with those of the other metrics tested (solely or combined; Appendix S4.3: Figures S4-3, S4-4, S4-5 and Tables S4-2, S4-3, S4-4), but better discriminated subgroups of populations in the classification tree (for further details, see Appendix S4.3: Figures S4-6, S4-7 and Table S4-5). Indeed, taking into account both individual distance traveled and space use, Intensity of Use was well suited to capture the expected alterations in movements of red deer and elk, plastically able to undertake both long-distance, directional movements and shorter, more tortuous ones (Peters et al., 2019; Rickbeil et al., 2019). Specifically, values of Intensity of Use close to 0 indicate either very straight movements or a very large occupied area, that is, the area covered by movements is wide with respect to the linear distance traveled (Figure 2, in purple). This would be the case for "narrow and wide ranges," covered by straight movements (e.g., long seasonal migrations) or a trajectory covering a very wide area (e.g., nomads or range shifts, Olson et al., 2010). Conversely, high Intensity of Use values represent an "excess" of linear movements with respect to the area covered, for example tortuous movements within a restricted area (e.g., residents, Figure 2, in orange).

2.4 | Assessing movement expression and its environmental drivers

2.4.1 | Modeling framework

To assess deer's movement expression dependence on environmental drivers, we used linear mixed-effect models with log-transformed Intensity of Use of red deer and elk as the response variable (Figure S4-1). First, to test whether Intensity of Use was affected more by the landscape scale environmental drivers than by the continental or species differences (Prediction 1.1), we used continent as a predictor (fixed or random intercept term). Then, to test the effect of landscape scale drivers on Intensity of Use, we fitted more complex models including environmental variables characterizing the landscape, specifically local topographic context (slope, Prediction 2.1; Figure 3a), resource predictability (NDVI predictability, Prediction 2.2; Figure 3b), and human activity (HFI, Prediction 2.3; Figure 3c). Due to strong variability in NDVI predictability and HFI within and across populations (Appendix S5: Figures S5-1 and S5-2; Appendix S6: Figures S6-1 and S6-2), we fitted population random slope terms for these two predictors. This also allowed us to better take into account movement expression variability at the local context (landscape) scale. Indeed, we kept the landscape and continental models separate to avoid confounding effects between scales. Furthermore, to test whether *high* human activity altered deer's responses, we alternatively fitted a threshold term for the HFI predictor (Prediction 2.4a), or a polynomial term of second order (Prediction 2.4b). The threshold level was identified as the change point at which the linear increase in Intensity of Use flattens despite an increase in HFI, using the chngpt R package (Fong et al., 2017). To account

for the autocorrelation introduced by repeated measures per individual, we added a random intercept term for individual identity in all models. We discarded altitude and terrain roughness index as potential covariates due to collinearity (Pearson's correlation coefficient: $|r| \geq .7$; Dormann et al., 2012).

2.4.2 | Model selection

We first selected the best continental scale model (Table S7-1). We then used a stepwise forward procedure to compare models of increasing complexity, from univariate to multiple predictors with random slope terms, and those with specific formulations (i.e., polynomial and threshold) for the HFI effect, to match our predictions (see Table S7.2). We iteratively retained those variable combinations with the lowest AIC, best goodness of fit (conditional and marginal R^2), and simplest model structure (Johnson, 2014) to identify the most parsimonious model to test Hypothesis 2 (Table S7.2). Finally, we compared the best continental scale and the best landscape scale models to test Hypothesis 1.

For completeness, we applied the most parsimonious model structure as per the above model selection, to the subsetted data for each continent (Table S7-3), and to the other movement metrics we earlier explored with the cluster analysis (total distance traveled; MaxDist: Table S7-4).

All analytical steps, including the preparation of animal GPS locations and environmental data, data manipulation, calculations of movement metrics, extraction of environmental variables, statistical analyses, and model selection were carried out in R (R Core Team, 2023) using the R packages cited above as well as *amt* (Signer et al., 2019), *lme4* (Bates et al., 2015), *jtools* (Long, 2020), and *raster* (Hijmans, 2023).

3 | RESULTS

3.1 | Human footprint and resource predictability varied across populations

Red deer and elk populations occupied heterogeneous areas in terms of topography (slope: from 0° to 68.49°, median = 9.19°, SD = 8.92°; Figure 3a) and NDVI vegetation predictability (from 0.24 to 1, median = 0.58, SD = 0.09; Figure 3b) when compared across all study sites. A wide range of HFI values was also observed (from 0 to 44.41, overall median = 2.25, SD = 6.0; Figure 3c); however, the range was complementary at the continental scale, with the North American populations being exposed to lower values of HFI (populations' medians from 0.25 to 3.32, overall North American median = 1.25, SD = 3.06; Figure 3c and Figures S5-1 and S5-2) than the European populations (populations' medians from 2.68 to 29.75, overall European median = 9, SD = 7.59; Figure 3c and Figures S5-1 and S5-2). Consequently, the univariate linear relationship between HFI and Intensity of Use fitted at the population scale was observed to be
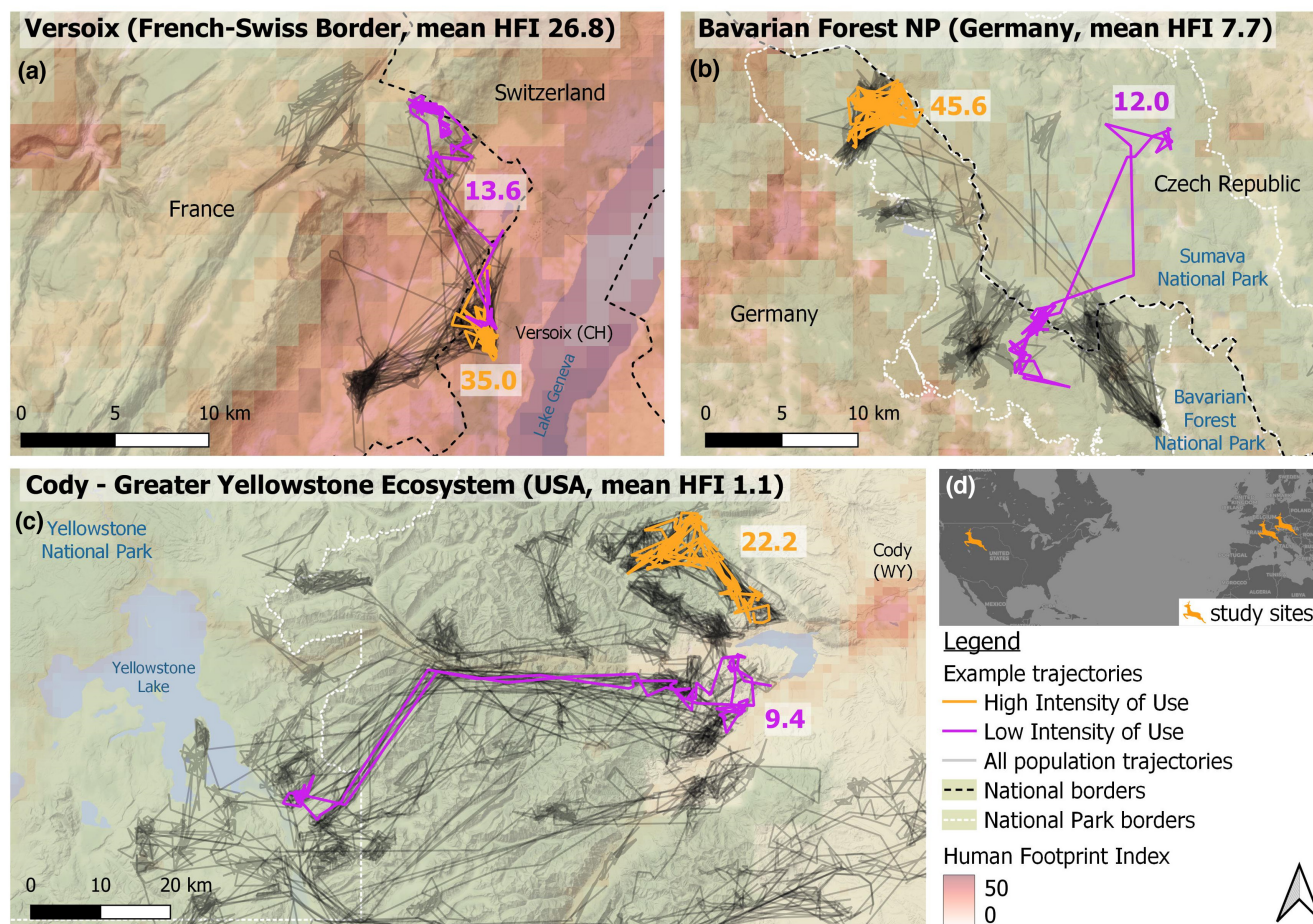
FIGURE 2 Examples of movement expression measured using the metric Intensity of Use. The GPS trajectories on the maps were chosen to illustrate the differences between low and high Intensity of Use values for more (purple) and less (orange) directional movements, respectively. The trajectories shown are those of red deer in Versoix on the French-Swiss border (a), the Bavarian Forest National Park in Southeast Germany and Sumava National Park in Czech Republic (b), and elk in Cody, Wyoming, Greater Yellowstone Ecosystem (c). Color-matched labels indicate the Intensity of Use values calculated for each shown trajectory as the average across all locations within the study period. Red shading indicates levels of Human Footprint Index (HFI); in the header of each map, the mean HFI values based on average HFI values across all available trajectories of the respective population are given. For easier readability, HFI and Intensity of Use values are shown in their original scale. The base map features hill shades and natural vegetation colors ("Stamen Terrain"; Stamen Design 2021). White dotted lines indicate the borders of national parks. Dashed black map lines delineate study areas and do not necessarily depict accepted national boundaries. Overview map at the bottom-right (d) indicates the location of the three populations used as examples.

highly variable (Figure S6-1). NDVI predictability values were also very variable across populations, although to a lower extent than what was observed for HFI (Figure S6-2).

3.2 | Environmental context and pressure of human activity affect movement expression

The most parsimonious model to explain the variation in Intensity of Use in dependence on landscape scale environmental variables performed substantially better than the best model solely based on continent as a fixed effect (ΔAIC = 112; Table S7-1), so supporting Hypothesis 1. This model included a negative association with NDVI predictability (Table S7-2, model 4.3; β = −0.022,

not significant, but improving model fit), but not slope, and, as the strongest effect, a threshold term for HFI; the random slope terms by population for NDVI and HFI were also included, indicating a strong landscape scale variability (Table S7-2, model 4.3). Hence, our results partially supported Hypotheses 2, in particular Predictions 2.2, 2.3, and 2.4a. Intensity of Use of red deer and elk movements increased until HFI = 6.6 (unscaled), beyond which the Intensity of Use was predicted to be constant (β = 0.630, $p < .01$; Table S7-2, model 4.3; Figure 4). Note that the threshold term did not persist as a significant factor for the same model formulation applied to continental-level subsetted data sets, especially for the North American subset (Table S7-3, model 1.1 and 1.2). Finally, when the best model structure was applied to the alternative movement metrics explored, HFI remained the most important
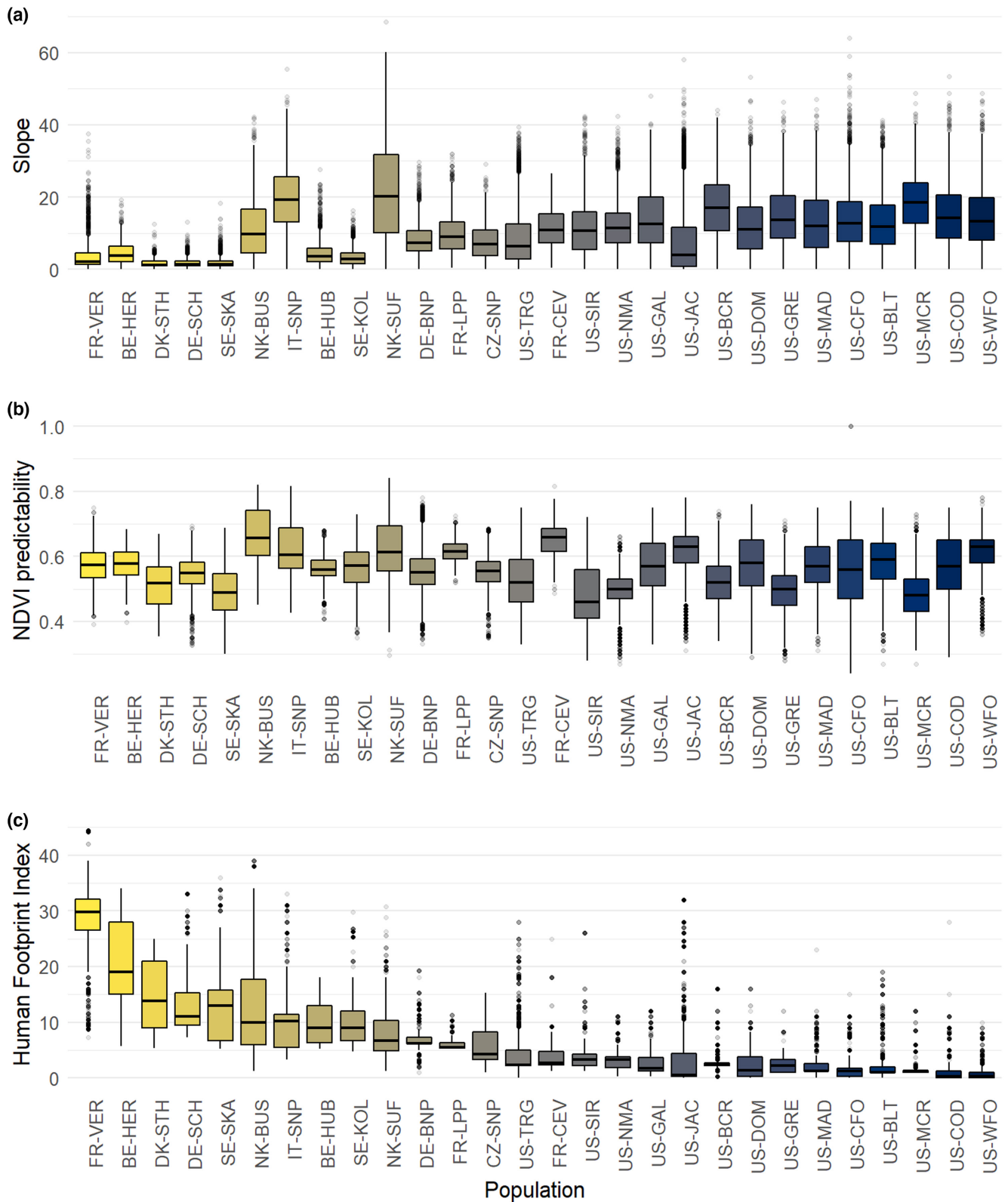
FIGURE 3 Variation of predictor variables for the 28 red deer and elk populations across Europe and the Greater Yellowstone Ecosystem. Shown are three measured environmental variables, specifically slope (a), normalized difference vegetation index (NDVI) predictability (b) and Human Footprint Index (HFI) (c). Single measurements are extracted at Global Positioning System (GPS) location level and then averaged at individual trajectory level, representing the average environmental condition individuals are exposed to along their trajectories (values shown are not scaled, whereas for all analytical steps environmental variables values were scaled to assure comparable results). For population code names, see Table S1-1. The populations are ordered by the HFI gradient (panel c, highest to lowest) in all panels (yellow to dark blue gradient).
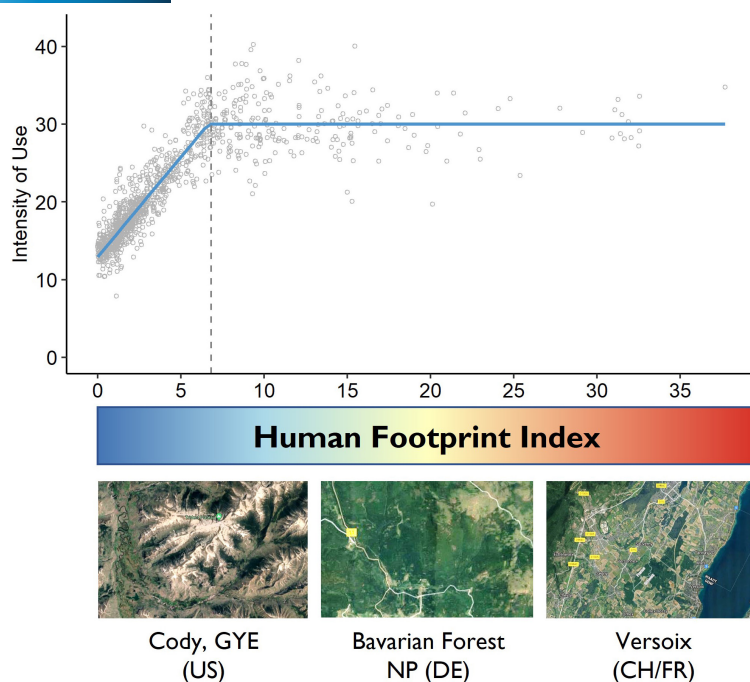
FIGURE 4 Model predictions of the best-fitting model indicating the effect of human activity on Intensity of Use (log-transformed) in red deer and elk. The model includes landscape-scale dependence of Intensity of Use on Human Footprint Index (HFI) and normalized difference vegetation index (NDVI) predictability as fixed effect terms (the former as a threshold term) and population-level random slopes. The plot shows the effect change in Intensity of Use relative to HFI, while NDVI predictability is kept constant (i.e., at mean value). The vertical dashed line indicates the threshold level identified in this study (HFI = 6.6, unscaled). Gray circles indicate average Intensity of Use values across each individual trajectory. For reference, we show three study areas with different levels of HFI (i.e., Cody, Greater Yellowstone Ecosystem: mean HFI = 1.1; Bavarian Forest NP: mean HFI = 7.7; Versoix: mean HFI = 26.8; Figure 2).

predictor, but the signs of the effects flipped, as expected using single distance measures, as opposed to the rate between path length and the area it occupies (Table S7-4).

4 | DISCUSSION

Our analysis demonstrated that human activity (measured as HFI) shaped movement expression of red deer and elk at the land-scape scale across the wide environmental gradients we studied. Compared across all populations, human activity was the strongest driver of movement expression, superseding the effect of resource predictability and topography (Prediction 2.3 vs Prediction 2.1 and 2.2). Overall, the landscape characteristics also better explained movement expression of elk and red deer than broad continental or species-specific differences (Prediction 1.1).

We found that both red deer and elk movement varied from highly segmented trajectories over relatively small areas (e.g., populations in Skane in Sweden- SE-SKA or Silver Run in Montana, USA—US-SIR; Table S1-1 and Figure 3c), to extended displacements across wide landscapes (e.g., Clark's fork in Wyoming, USA—US-CFO; Table S1-1 and Figure 3c), or directed transitions through restricted corridors (e.g., Versoix in Switzerland—FR-VER; Sunnfjord in Norway—NK-SUF and Wiggins Fork in Wyoming, USA—US-WFO; Table S1-1 and Figure 3c). By characterizing movement expression with a standard-ized movement metric reflecting both the extent and directionality

of movements (i.e., Intensity of Use), we were able to identify a continuum of movement tactics opposed to an often-assumed di-chotomization of movement into migratory and residential tac-tics (Ball et al., 2001; Cagnacci et al., 2011, 2016). We identified elk in the GYE expressing more directional movements than most European red deer populations (Figure S4-6 and Table S4-5), yet few of the latter shared movement expression traits with elk rather than with the other red deer populations (Figure S4-6a), sug-gesting that these species have very similar movement capacities (motion capacity sensu Nathan et al., 2008). More specifically, both species were able to travel similar distances (Figure S4-2): indeed, our models indicated that differences in movement expression were driven by the local environmental context (Eggeman et al., 2016, Peters et al., 2019) rather than broad continental scale or taxonomic differences (Prediction 1.1; Table S7.1 vs Table S7.2).

Our analyses demonstrated the impact of human activity as the strongest determinant of the observed continuum of movement responses in red deer and elk. Studies investigating at local scale consistently found that movements of red deer and elk were driven by plant phenology, snow cover and landscape topography (Bischof et al., 2012; Peters et al., 2019; Rickbeil et al., 2019). Our study may not suggest that human activity replaces these important drivers at local scales but that it may prevail over them at the landscape scale. For example, Aikens et al. (2020), using a similar set of populations to those considered in this study, showed a decreased performance in resource tracking (green wave surfing) in four ungulate species

ranging in landscapes under higher human activity. Looking across a wide range of terrestrial mammals, Tucker et al. (2018) observed a general reduction in long-distance movements as human activity (HFI) increased. In this work, by looking at large, multi-population data sets of two deer species we offer insights into the mechanisms underlying such a pattern. Deer responded to human activity within landscapes with increasingly truncated movements, yet such behavioral plasticity was constrained at relatively low values of human activity. We showed that the directionality of movements decreased steeply with increasing human activity and plateaued after reaching an identified threshold of HFI = 6.6 (unscaled) (Prediction 2.4a, Figure 4, Table S7-2 model 4.3).

This alteration of movement expression and reduction in behavioral plasticity may limit deer's resilience to further human induced modifications, ultimately affecting fitness and thus demographic parameters such as increased human infrastructure-related mortality (Prokopenko et al., 2017), or decreased accessibility of forage resources (Aikens et al., 2020). Conversely, anthropogenic landscapes may also offer concentrated and accessible resources that attract generalist and plastic herbivores such as deer (Middleton et al., 2013; Salvatori et al., 2023) or offer protection from predators according to the human shield hypothesis (Berger, 2007). In general, despite the growing body of evidence, the detailed underlying mechanisms of animal movement responses to anthropogenic pressure remain unclear. At the landscape scale, human activity and associated landscape modifications might reduce animal's *ability to move*, when fragmentation and anthropogenic infrastructure act as barriers (e.g., Beyer et al., 2016, Xu, Barker, et al., 2021) and further alter the *need to move* due to alternative sources of nutrition, for example, through access to irrigated agricultural production sites (Middleton et al., 2013) or anthropogenic supplemental feed (Jones et al., 2014; Ossi et al., 2017; Ranc et al., 2021). Taken together, human activity can fundamentally alter culturally learned movement tactics (Jesmer et al., 2018), formed in natural landscapes but shaped into patterns of restricted habitat use under pressure of human activity.

Notably, we had little observations to assess deer behavior at very high values of HFI, and only in Europe, probably because of few populations monitored or persisting in such conditions (median HFI for US populations: 1.2; for European populations: 9.0). Interestingly, the overall threshold model did not hold when applied to subsetted data sets for Europe and North America, a result possibly linked to the process underpinning animal responses to human activity (Table S7-3, models 1.1 and 1.2). Intensity of Use linearly increased with HFI for the North American populations when considered apart (Table S7-3, model 2.2), as well as for those European populations exposed to HFI in the range of the North American ones (Table S7-3, model 2.1). Conversely, Intensity of Use decreased as HFI increased for European populations exposed to higher HFI than what recorded in the GYE (Table S7-3, model 3.1; see for example the directed and constrained movements for Switzerland/France—FR-VER; Table S1-1 and Figure 3c). We interpret this decrease in Intensity of Use in highly fragmented and infrastructure-rich landscapes as being due to forays to reach disconnected suitable habitat patches within the

human-dominated matrix. These further results confirm, on the one side, the similar response of elk and red deer when exposed to similar levels of human activity; on the other side, they indicate that a clearer picture of the variation in movement expression only emerges when the entire range of HFI is considered, that is, across continents in case of this study. Incidentally, this underlines the importance of tracking wild species in more anthropogenic areas, including urban environments, to quantify and better predict anthropogenic impact on species (Rutz et al., 2020). Furthermore, to address complex and plastic movement responses under very high human activity, disturbance measures of higher resolution or dynamic nature would be appropriate, as it has been shown that HFI is not capturing fine scale human activities as, for example, fences or human mobility (Corradini et al., 2021; McInturff et al., 2020; Nickel et al., 2020).

In this work, we focused on spatial responses to human activity of *Cervus* spp. species, previously reported as behaviorally plastic (Peters et al., 2019; Rickbeil et al., 2019). Other deer and more in general wild ungulate species have shown highly diverse and less flexible responses, even when exposed to a narrower gradient and lower level of disturbance. For reindeer (*Rangifer tarandus*) in Norway, for example, infrastructure such as secondary roads and tourist cabins have a strong effect, potentially hindering access to migratory corridors and calving sites (Panzacchi, Van Moorter, Jordhøy, et al., 2013; Panzacchi, Van Moorter, & Strand, 2013). Pronghorn (*Antilocapra americana*), in turn, are particularly sensitive to fences and in only about 50% of encounters they have been found to cross them, demonstrating how strongly common human landscape modification can affect movement behavior of ungulates (Xu, Dejid, et al., 2021). Similarly, Mongolian gazelle decrease their average nomadic forays, especially in proximity of roads and as traffic volume increases (Mendgen et al., 2023). Long-term effects of human disturbances on fitness and demography often remain unclear, but it has been shown that, for example, gas and oil development and associated changes in the migratory corridors of mule deer in Wyoming, USA, led to altered movement behavior and even long-term negative trends in population abundance (Aikens et al., 2022; Sawyer et al., 2017). In general, a decline in migratory behavior is observed across several ungulate species (Harris et al., 2009; Kauffman et al., 2021). Thresholds of human activity inducing potential behavioral changes are expected to be highly variable among species and environmental context. Recent studies revealed that other widely distributed terrestrial mammal species other than ungulates are responding in complex ways to human activity and landscape modifications. For example, at the local scale, Creel et al. (2020) found a shift in movement behavior for wild dogs (*Lycaon pictus*) with reduced fast and straight movements in areas with high human activity with respect to protected areas, suggesting a decrease in connectivity. In addition, home range sizes, and assumingly the underlying movement patterns of the Holarctic distributed red fox (*Vulpes vulpes*), were found to be strongly altered by human activity at global scale (Main et al., 2020).

The impact of human activity especially on long-distance and directional movements of animals, as we also showcase in this work,

raises concerns about the consequences of human activity particularly for far-ranging species, such as partially migratory ungulates, or large carnivores (Doherty et al., 2021; Joly et al., 2019). The approach we implemented can broadly characterize the movement expression particularly in far-ranging and migratory species. Our approach, based on movement data processing using standardized and reproducible movement metrics, can be used to compare movement expression between individuals and populations and evaluate levels of truncation or alteration of movements, helping to identify the underlying process of how human encroachment affects the persistence of animal populations in changing landscapes. A better understanding of movement expression can facilitate the identification of appropriate management and conservation actions, for example, by identifying thresholds of human disturbance that alter movement behavior and space-use patterns. Either way, a truncation of long-distance movements in large-bodied primary consumers such as deer species has likely consequences on ecosystem functioning, for example, by limiting seed dispersal, nutrient cycling, and host–parasite dynamics (Bauer & Hoye, 2014). Even when deer are attracted by anthropogenic food, natural resources might still be preferred when accessible (Barker et al., 2019). The maintenance of corridors or connectivity habitats also in anthropogenic landscapes is therefore crucial to allow large herbivores' capacity to behaviorally respond to changing environmental conditions, instead of being limited to truncated movements. Conserving migratory species under globally increasing human impact, in particular, will depend on flexible and efficient tools to evaluate early warning signals, to mitigate current human impact on wildlife and to assess potential for restoration efforts in already degraded systems (Kauffman et al., 2021).

AFFILIATIONS

[1]Department of Biology and Biotechnologies "Charles Darwin", University of Rome La Sapienza, Rome, Italy

[2]Animal Ecology Unit, Research and Innovation Centre, Fondazione Edmund Mach, San Michele all'Adige, Italy

[3]Department of Environmental Science, Policy, and Management, University of California, California, Berkeley, USA

[4]NBFC, National Biodiversity Future Center, Palermo, Italy

[5]Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, Amsterdam, The Netherlands

[6]Department of Civil, Environmental and Mechanical Engineering (DICAM), University of Trento, Trento, Italy

[7]Stelvio National Park—Ersaf Lombardia, Bormio, Italy

[8]School of Computing, University of Wyoming, Wyoming, Laramie, USA

[9]Haub School of Environment and Natural Resources, University of Wyoming, Wyoming, Laramie, USA

[10]Idaho Department of Fish and Game, Idaho, Coeur d'Alene, USA

[11]Wildlife Sciences, Faculty of Forest Sciences and Forest Ecology, University of Goettingen, Goettingen, Germany

[12]US Fish and Wildlife Service, National Elk Refuge, Wyoming, Jackson, USA

[13]Université de Toulouse, INRAE, CEFS, Castanet Tolosan, France

[14]LTSER ZA PYRénées GARonne, Auzeville Tolosane, France

[15]National Park Service, Grand Teton National Park, Wyoming, Moose, USA

[16]Department of Nature Management, University of Applied Sciences of Western Switzerland, Jussy, Switzerland

[17]Montana Department of Fish, Wildlife and Parks, Montana, Helena, USA

[18]Department of Visitor Management and National Park Monitoring, Bavarian Forest National Park, Grafenau, Germany

[19]Chair of Wildlife Ecology and Management, Albert Ludwigs University Freiburg, Freiburg, Germany

[20]Inland Norway University of Applied Science Institute for Forest and Wildlife Management, Koppang, Norway

[21]Idaho Department of Fish and Game, Idaho, Boise, USA

[22]School of Business, Innovation and Sustainability, Halmstad University, Halmstad, Sweden

[23]U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Wyoming, Laramie, USA

[24]Natural and Agricultural Environmental Studies Department, Service Public de Wallonie, Gembloux, Belgium

[25]Wyoming Game and Fish Department, Wyoming, Jackson, USA

[26]Wyoming Game and Fish Department, Wyoming, Cody, USA

[27]Department of Biosciences, Centre for Ecological and Evolutionary Synthesis, University of Oslo, Oslo, Norway

[28]Department for Conservation, Biodiversity and Wildlife Management, Bavarian State Institute of Forestry, Freising, Germany

[29]Montana Department of Fish, Wildlife and Parks, Montana, Bozeman, USA

[30]Office Français de la Biodiversité, DRAS, "Montfort", Birieux, France

[31]Department of Ecoscience—Wildlife Ecology, Aarhus University, Aarhus, Denmark

[32]Šumava National Park, Vimperk, Czech Republic

AUTHOR CONTRIBUTIONS

SM, FC, ADM, and PC conceived the research and wrote the original manuscript; JDG and SM managed the data. SM, AC, and JDG analyzed the data and wrote the R/SQL code; ADM, GA, PA, EC, LD, SD, CF, JG, KP, MH, MH, NB, AJ, MJK, AL, DMW, TM, LP, NM, AM, SS, JS, PS, MS, and FC collected the data; SM and AC designed the maps. All authors reviewed and edited the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in zenodo at http://doi.org/10.5281/zenodo.7919725, reference number 7919725.

CAPTURE INFORMATION

Animal captures have been carried out by following institutions under protocol ensuring animal welfare. In the France-Versoix area, captures were conducted by the game keepers of the Direction Générale Nature et Paysage of Geneva. In Belgium (Hertogenwald and St-Hubert): Capture and GPS-collaring of wild game complied with the Regional law of Wallonia (M.B. 14.07.2011). All elk captured in Montana, USA were performed in accordance with Montana Fish, Wildlife, and Parks (MFWP) biomedical protocols for free-ranging Cervidae. Collaring and capture activities on the Jackson elk herd were authorized under Wyoming Chapter 33 permit number 33-394. The capture procedure of red deer in Sweden fulfilled ethical requirements and was approved by the Animal Ethics Committee of central Sweden (decisions M258-06 and 50-06). Capture and collaring of red deer in Denmark was authorized by the Danish Nature and Forest Agency (General institutional permission for capturing and marking birds and mammals, reference: SM 302-009). In the France-Versoix area, collaring and captures were authorized by the cantonal administration "Direction Générale Nature et Paysage." Capture and collaring or red deer in the Cévennes National Park in France was authorized by the Cévennes National Park and the French Ministry of Agriculture (certificate no. 7060 to Dominique Pépin). In the France, La Petite Pierre area, game captures were conducted in accordance with European and French laws. The experiment was designed to minimize animal stress and handling time and to ensure animal welfare, as defined in guidelines for the ethical use of animals in research. A specific accreditation was also delivered to the OFB for capturing animals for scientific and wildlife management purposes. Red deer captures and experimental procedures were in line with the French Environmental Code (Art.R421-15 to 421-31 and R422-92 to 422-94-1) and duly approved by legislation from the Prefecture of Paris (Prefectural decree no. 2009-014 and No. 2015-020). Captures and fitting deer with GPS radio collars in Stelvio National Park were authorized by the Ministry for Environment and Autonomous Province of Trento within the framework of Red deer Conservation and Management Project approved by ISPRA (National Institute for Environmental Protection and Research).

ORCID

Steffen Mumme https://orcid.org/0000-0002-3671-4596
Andrea Corradini https://orcid.org/0000-0002-9294-656X
Ellen O. Aikens https://orcid.org/0000-0003-0827-3006
Francesca Cagnacci https://orcid.org/0000-0002-4954-9980

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SUPPORTING INFORMATION

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