Title: Moving in the Anthropocene: Global reductions in terrestrial mammalian movements

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Animal movement is fundamental for ecosystem functioning and species survival, yet the effects of the anthropogenic footprint on animal movements have not been estimated across species. Using a unique GPS-tracking database of 803 individuals across 57 species, we found that mammalian movements in areas with a comparatively high human footprint were on average two-to-three times smaller than those in areas with a low human footprint. We attribute this reduction to both behavioral changes of individual animals and the exclusion of species with long-range movements from areas with higher human impact. Global loss of vagility alters a key ecological trait of animals that not only affects population persistence, but also ecosystem processes, such as predator-prey interactions, nutrient cycling, and disease transmission.

With approximately 50-70% of the Earth's land surface currently modified for human activities (*1*), patterns of biodiversity and ecosystem functions worldwide are changing (*2*). The expanding footprint of human activities is not only causing the loss of habitat and biodiversity, but also affects how animals move through fragmented and disturbed habitats. The extent to which animal movements are affected by anthropogenic changes in the structure and composition of landscapes and resource changes has only been explored in local geographic regions or within single species. Such studies typically report decreasing animal movements, for example due to habitat fragmentation, barrier effects or resource changes (*3–6*), with only a few studies reporting longer movements as a result of habitat loss or altered migration routes (*7*, *8*). Here we conducted a global comparative study examining how the human footprint affects movements of terrestrial non-volant mammals using Global Positioning System (GPS) location data of 803 individuals from 57 mammal species (Fig. 1 and Table S2). Mean species' mass ranged from 0.49 to 3940 kg and included herbivores, carnivores, and omnivores (n = 28, 11, and 18 species, respectively).

For each individual, we annotated locations with the Human Footprint Index (HFI), an index with a global extent that combines multiple proxies of human influence: the extent of built environments, crop land, pasture land, human population density, night-time lights, railways, roads and navigable waterways (*9*) (see Supplementary Methods for details). The HFI ranges from 0 (natural environments: e.g., the Brazilian Pantanal) to 50 (high-density built environments: e.g., New York City).

In addition to the human footprint, we included other covariates that are known to influence mammalian movements. First, mammals generally move farther in environments with lower productivity, because individuals may need to cover a larger area to gather sufficient resources (*10*). To capture this effect, we annotated locations with the Normalized Difference Vegetation Index (NDVI), a well-established, satellite-derived measure of resource abundance for herbivores and carnivores alike (*11*). Second, an allometric scaling relationship shows that animals of greater body size usually move farther (*12*), and third, diet may influence movements due to differences in foraging costs and availability of resource types (*13*, *14*). To capture these effects, we annotated the database with species averages for body size, and dietary guild (i.e., carnivore, herbivore or omnivore).

We then calculated displacements as the distance between subsequent GPS locations of each individual at nine time scales (*15*) ranging from one hour to ten days. For each individual at each time scale, we calculated the 0.5 and the 0.95 quantiles of displacement. The combination of different time scales and quantiles allowed us to examine the effect of the human footprint on both the median (0.5 quantile) and long-distance (0.95 quantile) movements for within-day movements (e.g., 1-hour time scale) up to longer time displacements of over one week (e.g., 10-day time scale). We used linear mixed effects models that, in addition to all covariates (i.e., NDVI, body mass, diet), also accounted for taxonomy and spatial autocorrelation (see Supplementary Methods for details).

We found strong negative effects of the human footprint on median and long-distance displacements of terrestrial mammals (Fig. 2a and b, Fig. 3a and Supplementary Table S3). Displacements of individuals (across species) living in areas of high human footprint (HFI = 36) were up to three times shorter than displacements of individuals living in areas of low human footprint (HFI = 0). For example, median displacements over ten days were 3.3 km (± SE: 1.4 km) in areas of high human footprint vs. 6.9 km (± SE: 1.3 km) in areas of low footprint (Fig. 2a, Table Supplementary Table S3). Likewise, the maximum displacement distances at the 10-day scale averaged 6.6 km (± SE: 1.4 km) in areas of high vs. 21.5 km (± SE: 1.4 km) in areas of low human footprint (Fig. 2a, Supplementary Table S3). The effect was significant on all temporal scales with more than eight hours between locations.

The effect was not significant at shorter time scales (Fig. 3a, 1 - 4h), suggesting that the human footprint affects ranging behavior and area use over longer time scales, rather than altering individual travel speeds (i.e., individuals may travel at the same speed if measured across short time intervals, but have more tortuous movements in areas of higher human footprint and thus remain in the same locale if displacement is measured across longer time intervals).

Reduction in movement may be due to an (1) individual-behavioral effect, where individuals alter their movements relative to the human footprint, or (2) a species-occurrence effect, where certain species that exhibit long-range movement simply do not occur in areas of high human footprint. To disentangle these two effects, we ran additional models where we separated the HFI into two components: (1) the individual-behavioral effect represented by the individual variability of HFI relative to the species mean (i.e., the individual HFI minus the species mean HFI), and (2) the species-occurrence effect as the mean HFI for each species.

Results from the two-component model indicate behavioral as well as species effects. We found a significant behavioral effect on median displacements and on long-distance displacements (0.95 quantiles) at most timescales (from eight hours to ten days) (Supplementary Fig. 2a, Supplementary Table S4). The species-occurrence effect was significant only over longer timescales (128 and 256 hour periods or 5 and 10 days, respectively) (Supplementary Fig. 2b, Supplementary Table S4). However, we note that the estimate of the species-occurrence effect is conservative because our model incorporated taxonomy as a random effect. Some variability in the data may have been accounted for by the species-level random effect rather than the species-level HFI (see Table S3).

In addition to the human footprint effect, body mass, dietary guild, and resource availability were also related to movement distances. First, as expected from allometric scaling and established relationships of body size with home range size (*14*) and migration distance (*16*), larger species travelled farther than smaller species (Fig. 3c, Supplementary Table S3 and S4). Second, we found a negative relationship between resource availability and displacement distance such that movements were on average shorter in environments with higher resources (Fig. 3b, Supplementary Table S3 and S4). These results are consistent with reports of larger home range size (*17*) and longer migration distance (*18*) in mammals living in resource-poor environments. Finally, our analyses showed that carnivores travelled on average farther per unit time than herbivores and omnivores (Supplementary Table S3 and S4). These results concur with prior understanding that carnivores have larger home range sizes (*14*) because they need to find mobile prey and compensate for energy conversion loss through the food web. For all of these variables, effects were significant across time scales longer than eight hours for both median and long-distance displacements.

The reduction of mammalian movements in areas of high HFI likely stems from two non-exclusive mechanisms; 1) movement barriers such as habitat change and fragmentation (*19*, *20*); and 2) reduced movement requirements due to enhanced resources (e.g., crops, supplemental feeding and water sources (*5*, *21*)). Studies have shown both mechanisms at work with varying responses across populations or species (see Supplementary Table S5 for examples). In some cases, they act together on single individuals or populations – for example, red deer in Slovenia have smaller home ranges due to the enhancement of resources via supplemental feeding and the disturbance and fragmentation caused by the presence of roads (*22*).

While these mechanisms can have differential effects on population densities (i.e., increases under supplementation (*23*) and decreases under fragmentation (*24*)) the consequences of reduced vagility affects ecosystems regardless of the underlying mechanisms and go far beyond the focal individuals themselves. Animal movements are essential for ecosystem functioning as they act as mobile links (*25*) and mediate key processes such as seed dispersal, food-web dynamics including herbivory and predator-prey interactions, and metapopulation- and disease dynamics (*26*). Single species or single site studies have shown the severe effects of reduced vagility on these processes (*27*, *28*). The global nature of reduced vagility across mammalian species that we demonstrate here suggests consequences for ecosystem functioning worldwide. Future landscape management should include animal movements as a key conservation metric and aim towards maintaining landscape permeability. Ultimately, because of the critical role of animal movement for human-wildlife coexistence (*29*) and disease spread (*30*), effects of reduced vagility may go beyond ecosystem functioning and directly affect human well-being.

Figures

Fig. 1 Locations from the GPS tracking database and the Human Footprint Index. (A) GPS relocations of 803 individuals across 57 species plotted on the global map of the Human Footprint Index (HFI) spanning from 0 (low; yellow) to 50 (high; red). **(B)** Examples of the landscapes under different levels of HFI; 2 HFI (the Pantanal, Brazil), 20 HFI (Bernese Alps, Switzerland), 30 HFI (Freising, Germany), and 42 HFI (Albany, New York State, U.S.A.). **(C)** Species averages of 10-day long-distance displacement (0.95 quantiles of individual displacements).

Fig. 2 Mammalian displacement in relation to the Human Footprint Index. (A) Median and **(B)** long-distance (0.95 quantile) displacements decline with increasing Human Footprint Index at the 10-day scale (n = 48 species and 624 individuals). Plots include a smoothing line from a locally weighted polynomial regression. A Human Footprint Index of 0 indicates areas of low human footprint, and a value of 40 represents areas of high human footprint.

Fig. 3 Model coefficients (± CI) of linear mixed effects models predicting mammalian displacements using the (A) Human Footprint Index (HFI), (B) Normalized Difference Vegetation Index (NDVI), and (C) body mass. Models were run for the median (blue) and long-distance (0.95 quantiles; red) displacements of each individual calculated across different time scales. When the error bars cross the horizontal line the effect is not significant. See Supplementary Tables S3 for details.

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Supplementary Materials:

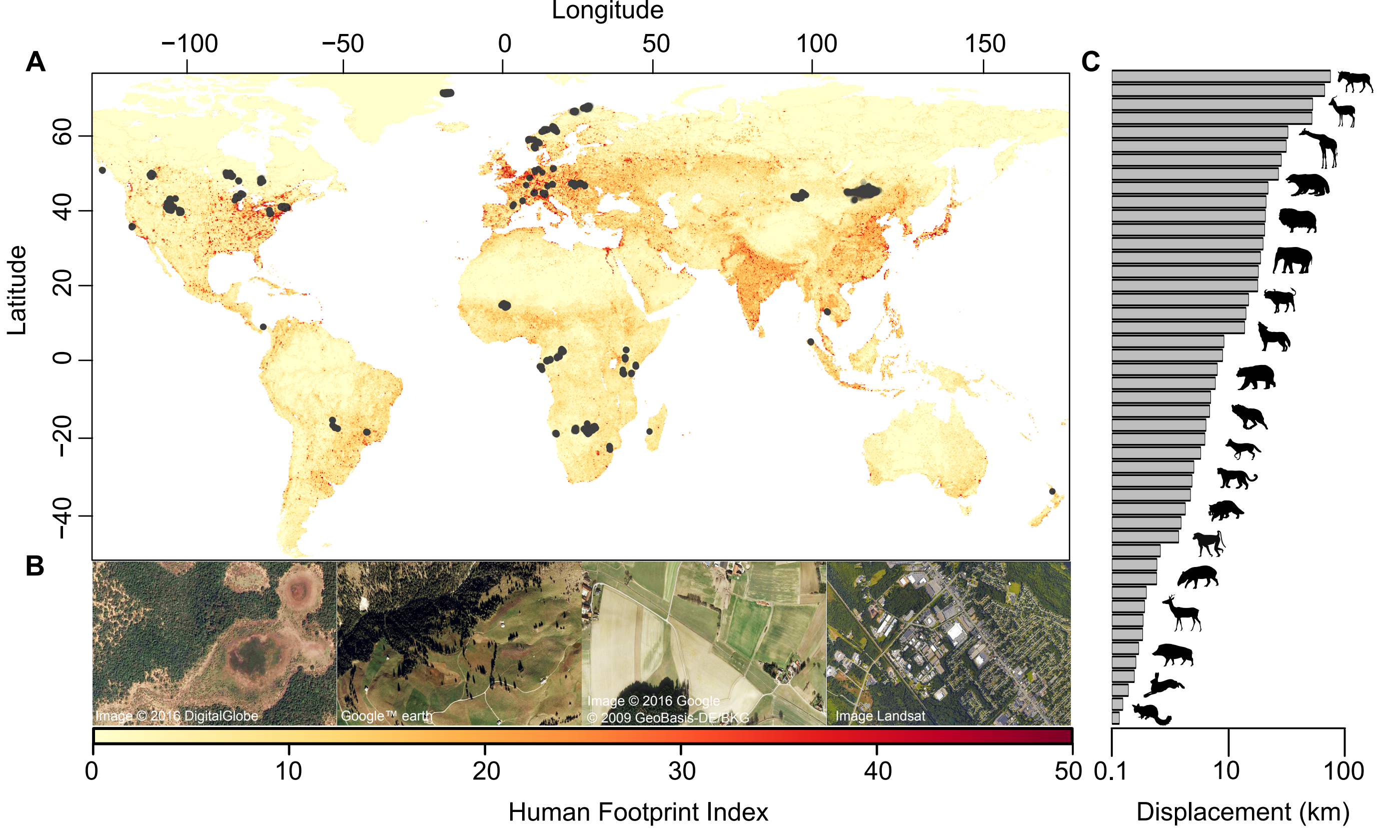
Materials and Methods

Supplementary Text

Figures S1-S2

Tables S1-S5

References (*31*-*89*)



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Latitude
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B
Image © 2016 DigitalGlobe
Google™ earth
Image © 2016 Google
© 2009 GeoBasis-DE/BKG
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Human Footprint Index
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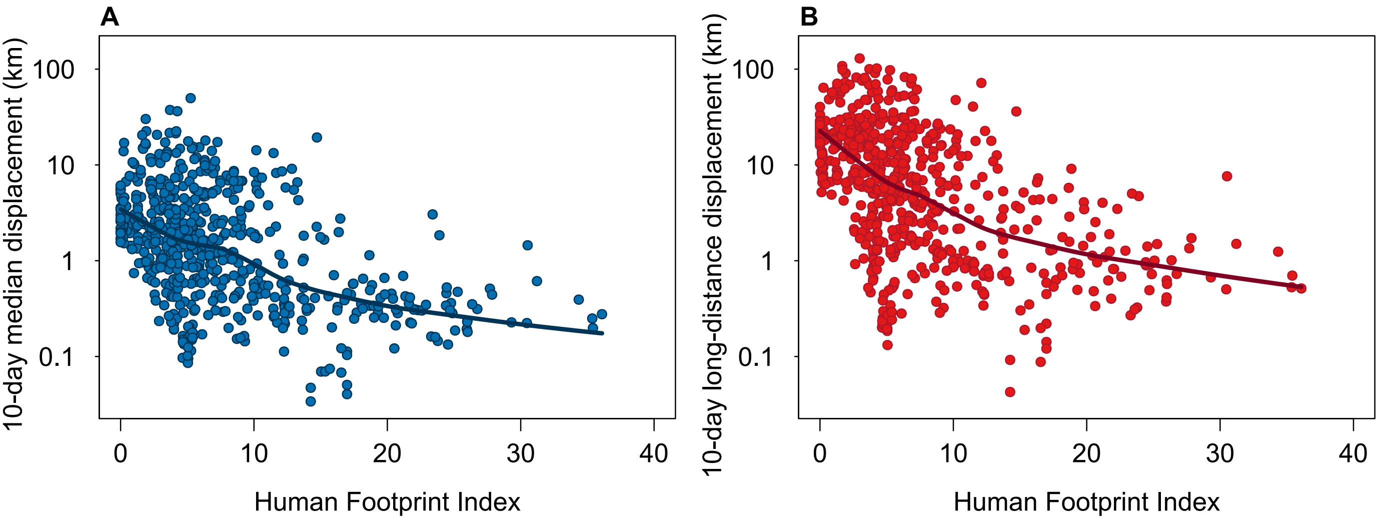
10
100
Displacement (km)



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10-day median displacement (km)
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10
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40
Human Footprint Index
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10-day long-distance displacement (km)
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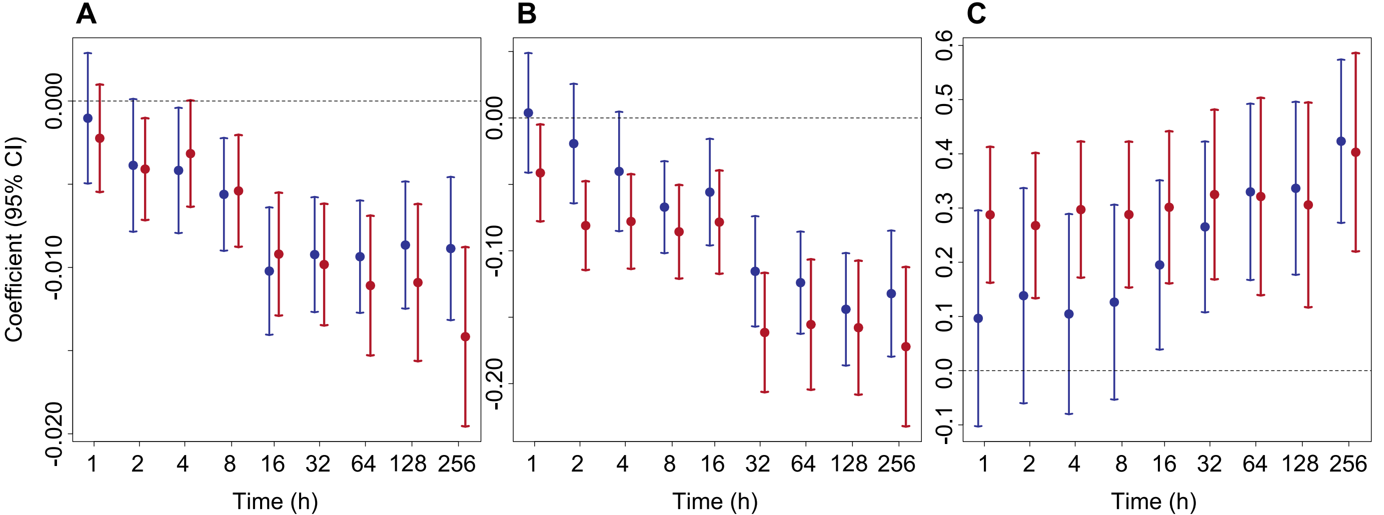
30
40
Human Footprint Index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Supplementary Materials for

Moving in the Anthropocene: Global Reductions in Terrestrial Mammalian Movements

Marlee A. Tucker, Katrin Böhning-Gaese, William F. Fagan, John M. Fryxell, Bram Van Moorter, Susan C. Alberts, Abdullahi H. Ali, Andrew M. Allen, Nina Attias, Tal Avgar, Hattie Bartlam-Brooks, Bayarbaatar Buuveibaatar, Jerrold L. Belant, Alessandra Bertassoni, Dean Beyer, Laura Bidner, Floris M. van Beest, Stephen Blake, Niels Blaum, Chloe Bracis, Danielle Brown, PJ Nico de Bruyn, Francesca Cagnacci, Justin M. Calabrese, Constança Camilo-Alves, Simon Chamaillé-Jammes, Andre Chiaradia, Sarah C. Davidson, Todd Dennis, Stephen DeStefano, Duane Diefenbach, Iain Douglas-Hamilton, Julian Fennessy, Claudia Fichtel, Wolfgang Fiedler, Christina Fischer, Ilya Fischhoff, Christen H. Fleming, Adam T. Ford, Susanne A. Fritz, Benedikt Gehr, Jacob R. Goheen, Eliezer Gurarie, Mark Hebblewhite, Marco Heurich, A. J. Mark Hewison, Christian Hof, Edward Hurme, Lynne A. Isbell, René Janssen, Florian Jeltsch, Petra Kaczensky, Adam Kane, Peter Kappeler, Matthew Kauffman, Roland Kays, Duncan Kimuyu, Flavia Koch, Bart Kranstauber, Scott LaPoint, Peter Leimgruber, John D. C. Linnell, Pascual López-López, A. Catherine Markham, Jenny Mattisson, Emilia Patricia Medici, Ugo Mellone, Evelyn Merrill, Guilherme de Miranda Mourão, Ronaldo G. Morato, Nicolas Morellet, Thomas A. Morrison, Samuel L Díaz-Muñoz, Atle Mysterud, Dejid Nandintsetseg, Ran Nathan, Aidin Niamir, John Odden, Robert B. O'Hara, Luiz Gustavo R. Oliveira-Santos, Kirk A. Olson, Bruce D. Patterson, Rogerio Cunha de Paula, Luca Pedrotti, Björn Reineking, Martin Rimmler, Tracey L. Rogers, Christer Moe Rolandsen, Christopher S. Rosenberry, Daniel I. Rubenstein, Kamran Safi, Sonia Saïd, Nir Sapir, Hall Sawyer, Niels Martin Schmidt, Nuria Selva, Agnieszka Sergiel, Enkhtuvshin Shiilegdamba, João Paulo Silva, Navinder Singh, Erling J. Solberg, Orr Spiegel, Olav Strand, Siva Sundaresan, Wiebke Ullmann, Ulrich Voigt, Jake Wall, David Wattles, Martin Wikelski, Christopher C. Wilmers, John W. Wilson, George Wittemyer, Filip Zięba, Tomasz Zwijacz-Kozica, Thomas Mueller
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Materials and Methods

Displacement Data

We compiled GPS location data for 57 mammalian species, comprising 7 339 376 locations of 803 individuals from 1998 to 2015 (Fig. 1, Supplementary Table S1). The dataset included adult male and female individuals. Datasets were obtained from the online animal tracking database *Movebank* (https://www.movebank.org/), the Movebank Data Repository (*Equus quagga* (*31*, *32*) and *Loxodonta africana* (*33*, *34*)), or were contributed by co-authors directly (Table S2). For species that are inactive at night (e.g., primates sleeping overnight in trees) and where the GPS devices had been switched off to prolong battery life, we interpolated location data during the inactive phase (i.e., using the last recorded position) with the same sampling frequency as that employed for active periods to ensure an even sampling regime.

We sub-sampled the location data with inter-location intervals at a geometric time scale from one hour to ~ ten days (i.e. 1, 2, 4, 8, 16, 32, 64, 128 and 256 hours) using the "SyncMove" R package (*35*). We started the sub-sampling algorithm from the first location recorded for each individual. For each of the nine time scales, we calculated the geodesic distance between the subsampled locations using the Spherical Law of Cosines using 6371 km as the mean radius of the Earth (*36*). This allowed a systematic investigation across time scales from within day movements to more long-term movements, and standardized the sampling regime across studies and individuals. Smaller time intervals were not available for most species and longer time intervals resulted in a significant loss in sample size. Sub-sampling precision was set to the inter-location interval ± 4% (e.g., for the 1-hour scale resulting in inter-location intervals varying between 57 and 62 minutes). We then checked the data for outliers, specifically for maximum movement speeds that were unlikely for a terrestrial land mammal to achieve over a given time period (> 4 m s^{-1}), and removed them (*37*). We calculated two response variables for each individual: the 0.5 quantile displacement distance and the 0.95 quantile displacement distance, the former describing the median movement behavior of that individual, and the latter describing long-distance movements (Supplementary Figure S1). All values were $\log_{10}$ transformed prior to analyses.

Covariates

We annotated each GPS location with NDVI and human footprint index (*38*) (HFI; Supplementary Table S2). NDVI data was extracted from MODIS Land Terra Vegetation Indices 500-m 16-day resolution (MOD13A1 V005 (*39*)) using the Movebank Env-DATA system (*40*) (environmental-data automated track annotation; http://www.movebank.org). We filtered the NDVI data to remove pixels with no data (-1), snow/ice (2) and clouds (3). We also included species body mass using the PanTHERIA database (*41*) (where individual mass information was unknown) and diet (i.e., carnivore, herbivore or omnivore) (Table S1). Body mass values were $\log_{10}$ transformed and the NDVI values were scaled. We then calculated the mean NDVI and human footprint value for each inter-location interval (i.e., the average value between each sequential pair of locations) and averaged these values for each individual.

Analyses

Our final database (Supplementary Fig. 1) comprised nine median and nine 0.95 quantile movement distance values for each individual (one for each temporal scale), associated with nine mean values for body mass, NDVI, and the human footprint index. We only included individuals that had tracking data for a minimum of two months (~60 days) or 50 displacements. We ran 18 linear mixed effects models, two for each time-scale, one with the 0.5 and the other with the 0.95 quantile displacement distances as the dependent variable, and body mass, NDVI, HFI, and diet as the predictor variables. We included species identity as a nested random effect to account for taxonomy (i.e., Order/Family/Genus/Species), and a Gaussian spatial autocorrelation structure (*42*) including the mean longitude and latitude for each individual. For each model, we checked the residuals for normality (i.e., Q-Q plots) and removed outliers (< 2% of total data points). All correlation coefficients among the predictor variables were $|r| \leq 0.55$ and all variance inflation factors (VIFs) were ≤ 2, well below the common cut-off values of 0.7 and 4, respectively (*43*, *44*). All model predictions and associated standard errors were calculated using the "AICcmodavg" R package (*45*). All analyses were performed in R version 3.2.2 (*46*).

Supplementary Text

Extended List of Acknowledgements

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Research. Movebank is hosted by the Max Planck Institute for Ornithology and the Movebank Data Repository is hosted by the University of Konstanz. Roe and red deer data were obtained from euroungulates, www.euroungulates.org. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Figure 1 silhouettes by J. A. Venter, H. H. T. Prins, D. A. Balfour & R. Slotow (vectorized by T. M. Keesey) (hare and buffalo) and R. Groom (gazelle) were downloaded from www.phylopic.org are available for re-use under the Creative Commons Attribution 3.0 Unported license. Figure 1 silhouettes by S. Traver (boar, deer, tapir, wildcat, elephant, muskox, wolverine, giraffe and khulan), O. Jones (baboon), D. Orr (coyote), T. Heath (bear and wolf) and G. Prideaux (possum) were downloaded from www.phylopic.org and are available for re-use under the Public Domain Mark 1.0 license. Leopard and maned wolf silhouettes by M. Tucker.

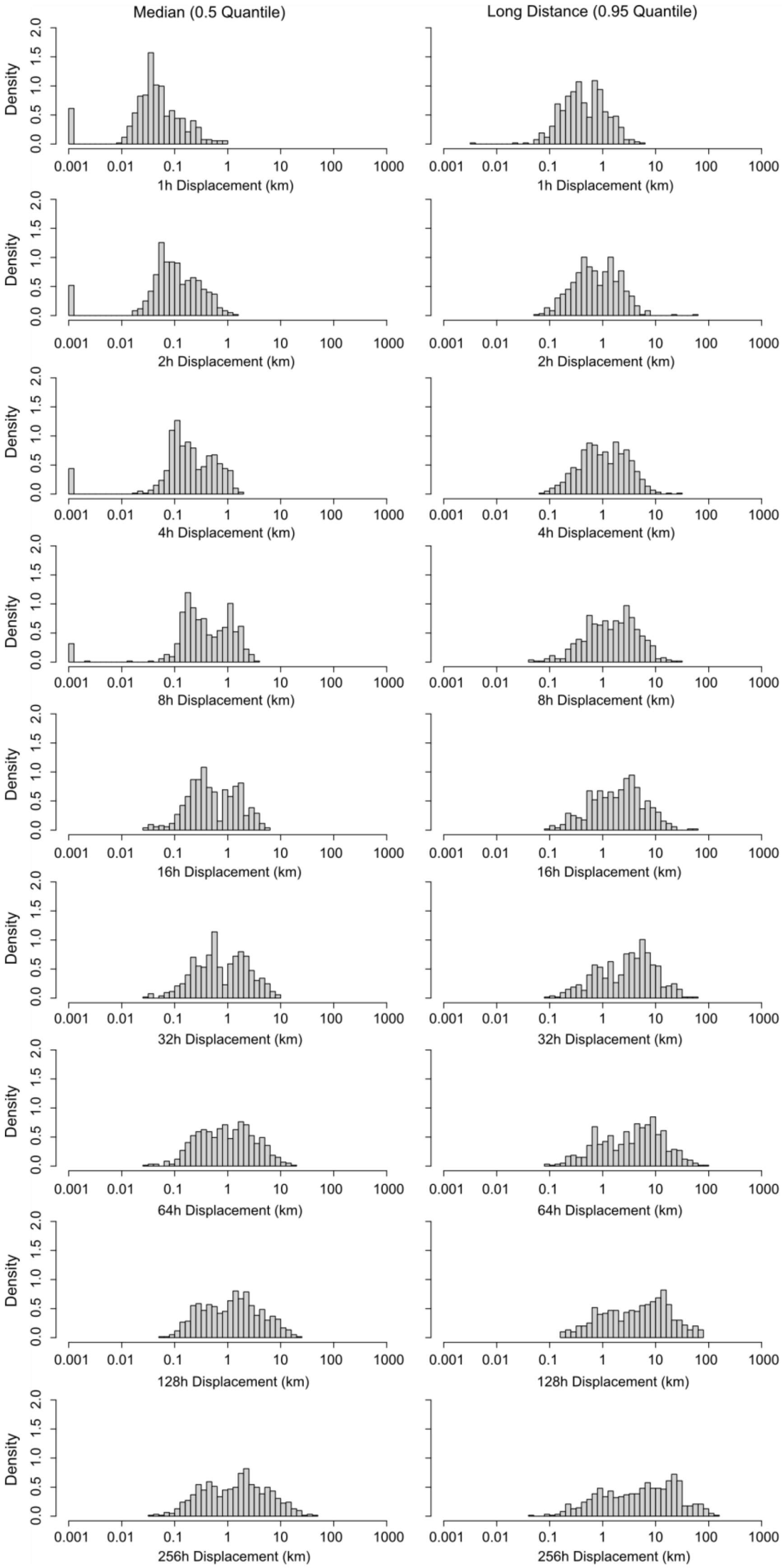

Fig. S1.

Distributions of the median and 0.95 quantiles of the individual displacements used in the analyses. The y-axis represents the density distribution of median (0.5 quantile) and long-distance (0.95 quantile) displacements of each individual.

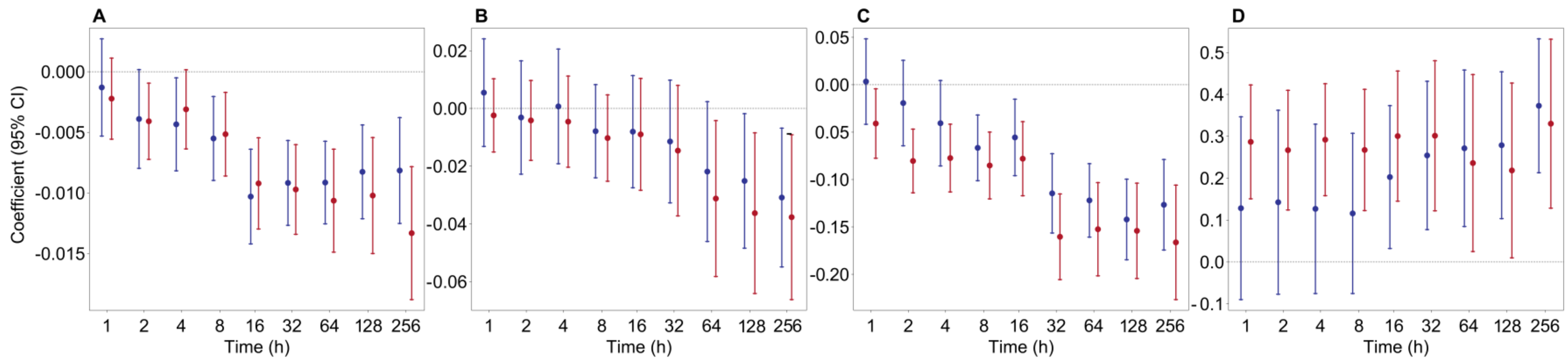

Fig. S2

Model coefficients (± CI) predicting mammalian displacements including (A) an individual-behavioral effect and (B) a species-occurrence effect of the Human footprint index (HFI). The individual-behavioral HFI was calculated as the individual HFI minus the species mean HFI, and the species-occurrence HFI was calculated as the species mean HFI. Other covariates of the model included (**C**) Normalized Difference Vegetation Index (NDVI), (**D**) body mass, and dietary guild (not shown). The models also included a nested random effect accounting for taxonomy, and a Gaussian spatial autocorrelation structure. Models were run for the median (i.e. -0.5 quantiles; blue) and long-distance (i.e. 0.95 quantiles; red) displacements of each individual calculated across different time scales. When the error bars cross the horizontal line (at 0) the effect is not significant. See Methods and Supplementary Tables S4 for additional details.

Table S1.

Data annotation summary

Variable	Unit	Temporal Resolution	Spatial Resolution	Source	Transformation
Normalised Difference Vegetation Index (NDVI)	Unitless	16 days	500 m	MODIS Land Terra Vegetation Indices 500-m 16-day (MOD13A1 V005)	Scaled
Human Footprint	Unitless	1993-2009 mean	1 km	Global terrestrial Human Footprint maps for 1993 and 2009 (*38*, *9*)	Log_{10}
Body Mass	Grams	Not applicable.	Not applicable.	K. E. Jones *et al.*, PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*. **90**, 2648 (2009).	Log_{10}
Diet	Unitless, categorical	Not applicable.	Not applicable.	K. E. Jones *et al.*, PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*. **90**, 2648 (2009).	Not applicable.

Table S2.
Summary of species and number of individuals per species included in the analyses.

Species	No. Individuals	Data Source	Species	No. Individuals	Data Source
Aepyceros melampus	20	Co-author	*Madoqua guentheri*	15	Co-author
Alces alces	46	Co-author	*Martes pennanti*	13	Movebank
Antilocapra americana	25	Co-author	*Myrmecophaga tridactyla*	4	Co-author
Beatragus hunteri	4	Co-author	*Odocoileus hemionus*	25	Co-author
Canis aureus	1	Movebank	*Odocoileus hemionus columbianus*	14	Co-author
Canis latrans	19	Movebank	*Odocoileus virginianus*	30	Movebank
Canis lupus	12	Co-author & Movebank	*Ovibos moschatus*	14	Co-author
Capreolus capreolus	94	Eurodeer & co-author	*Panthera leo*	2	Movebank
*Cercocebus galeritus**	1	Co-author	*Panthera onca*	4	Co-author
Cerdocyon thous	10	Co-author	*Panthera pardus*	4	Movebank
Cervus elaphus	47	Co-author, Eurodeer & Movebank	*Papio anubis*	4	Movebank
Chlorocebus pygerythrus	12	Movebank	*Papio cynocephalus**	22	Co-author & Movebank
Chrysocyon brachyurus	12	Movebank	*Procapra gutturosa*	15	Co-author
Connochaetes taurinus	3	Co-author	*Procyon lotor*	9	Movebank
Dasypus novemcinctus	1	Co-author	*Propithecus verreauxi**	28	Co-author
Elephas maximus	2	Movebank	*Puma concolor*	6	Co-author
Equus grevyi	7	Movebank	*Rangifer tarandus*	14	Co-author
Equus hemionus	6	Co-author	*Saguinus geoffroyi**	3	Movebank
Equus quagga	27	Co-author & Movebank	*Saiga tatarica*	3	Co-author
Eulemur rufifrons	4	Co-author	*Sus scrofa*	26	Co-author
Euphractus sexcinctus	7	Co-author	*Syncerus caffer*	6	Movebank
Felis silvestris	5	Movebank	*Tamandua mexicana*	2	Movebank
Giraffa camelopardalis	5	Co-author	*Tapirus terrestris*	4	Co-author
Gulo gulo	5	Co-author	*Tolypeutes matacus*	5	Co-author
Lepus europaeus	39	Movebank	*Trichosurus vulpecula**	29	Co-author
Loxodonta africana	14	Co-author & Movebank	*Ursus americanus*	21	Movebank
Loxodonta africana cyclotis	23	Movebank	*Ursus arctos*	13	Co-author
Lynx lynx	6	Co-author	*Vulpes vulpes*	5	Movebank
Lynx rufus	6	Movebank			

* GPS devices turned off during inactive periods to save battery (e.g., primates sleeping overnight in trees) and location data was interpolated during the stationary phases (see Methods in main text).

Table S3.

Model coefficients, r-squared and sample sizes of linear mixed effects models predicting the median and 0.95 quantiles of individual displacements from 1 to 256 hour time scales. Predictor variables included body mass, NDVI, diet and the human footprint index. The model also included a nested random effect accounting for the taxonomy, and a Gaussian spatial autocorrelation structure. We calculated the marginal r^2 (variance explained by the fixed effects) and conditional r^2 (variance explained by both fixed and random factors) values for each model using the “MuMIn” R package (*47*). Fixed effects included mass, NDVI, the human footprint index and diet. Random effects included taxonomy. *p<0.05, **p<0.01, ***p<0.001

	1h		2h		4h		8h		16h		32h		64h		128h		256h	
	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%
Mass	0.147	0.291***	0.169	0.274***	0.114	0.309***	0.141	0.315***	0.252***	0.335***	0.314***	0.358***	0.345***	0.374***	0.355***	0.368***	0.426***	0.44***
NDVI	0.004	-0.042*	-0.019	-0.082***	-0.04	-0.078***	-0.067***	-0.085***	-0.053*	-0.078***	-0.113***	-0.161***	-0.125***	-0.157***	-0.144***	-0.158***	-0.134***	-0.174***
HumanF	-0.001	-0.002	-0.004	-0.004*	-0.004*	-0.003	-0.006**	-0.005**	-0.01***	-0.009***	-0.009***	-0.01***	-0.009***	-0.011***	-0.009***	-0.011***	-0.009***	-0.014***
Diet (H)	0.082	-0.232	0.099	-0.194	-0.022	-0.433*	-0.03	-0.639**	-0.607**	-0.621**	-0.789***	-0.727**	-0.735**	-0.646**	-0.655**	-0.501*	-0.641**	-0.561**
Diet (O)	0.112	-0.138	0.026	-0.077	-0.007	-0.227	0.069	-0.364*	-0.29	-0.341*	-0.454*	-0.489*	-0.513*	-0.544*	-0.515*	-0.485*	-0.493*	-0.494*
r^2 Marginal	0.05	0.321	0.062	0.291	0.021	0.415	0.03	0.482	0.427	0.523	0.513	0.539	0.454	0.457	0.457	0.397	0.486	0.456
r^2 Conditional	0.892	0.852	0.913	0.885	0.95	0.878	0.973	0.898	0.864	0.883	0.897	0.896	0.902	0.865	0.867	0.835	0.86	0.829
Species	52		53		48		45		42		41		43		46		48	
Individuals	531		606		601		544		525		526		590		598		624	

Table S4.

Model coefficients, r-squared and sample sizes of linear mixed effects models predicting the median and 0.95 quantiles of individual displacements from 1 to 256 hour time scales. Predictor variables included body mass, NDVI, diet and the human footprint index, which was split into the individual-behavioral effect (Ind_HumanF: the individual HFI minus the species mean HFI) and species-occurrence effect (Sp_HumanF: the species mean HFI). The model also included a nested random effect accounting for the taxonomy, and a Gaussian spatial autocorrelation structure. We calculated the marginal r^2 (variance explained by the fixed effects) and conditional r^2 (variance explained by both fixed and random factors) values for each model using the "MuMIn" R package(*48*). Fixed effects included mass, NDVI, the human footprint index and diet. Random effects included taxonomy. *p<0.05, **p<0.01, ***p<0.001

	1h		2h		4h		8h		16h		32h		64h		128h		256h	
	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%
Mass	0.182	0.29***	0.172	0.276***	0.136	0.31***	0.132	0.306***	0.266***	0.341***	0.319***	0.354***	0.313***	0.327***	0.325***	0.32***	0.379***	0.394***
NDVI	0.003	-0.042*	-0.019	-0.082***	-0.041	-0.078***	-0.067***	-0.084***	-0.054*	-0.078***	-0.114***	-0.161***	-0.123***	-0.153***	-0.141***	-0.154***	-0.128***	-0.167***
Ind_HumanF	-0.001	-0.002	-0.004	-0.004*	-0.004*	-0.003	-0.006**	-0.005**	-0.01***	-0.009***	-0.009***	-0.01***	-0.009***	-0.011***	-0.008***	-0.01***	-0.008***	-0.013***
Sp_HumanF	0.006	-0.002	-0.003	-0.004	0.001	-0.003	-0.008	-0.008	-0.006	-0.007	-0.008	-0.011	-0.02	-0.026	-0.021	-0.03*	-0.03*	-0.035*
Diet (H)	0.054	-0.232	0.097	-0.195	-0.028	-0.433*	-0.038	-0.648**	-0.61**	-0.622**	-0.788***	-0.728**	-0.745**	-0.656**	-0.683**	-0.53*	-0.674**	-0.587**
Diet (O)	0.106	-0.138	0.023	-0.078	-0.019	-0.227	0.065	-0.376*	-0.292	-0.34*	-0.454*	-0.49*	-0.512*	-0.546*	-0.524**	-0.489*	-0.507*	-0.507*
r^2 Marginal	0.055	0.321	0.061	0.291	0.021	0.416	0.031	0.492	0.417	0.52	0.509	0.542	0.491	0.497	0.507	0.455	0.558	0.519
r^2 Conditional	0.892	0.852	0.913	0.885	0.95	0.878	0.973	0.901	0.859	0.882	0.895	0.897	0.908	0.877	0.877	0.852	0.876	0.845
Species	52		53		48		45		42		41		43		46		48	
Individuals	531		606		601		544		525		526		590		598		624	

Table S5.

Summary of the positive (+) and negative (-) effects of barriers and anthropogenic resources on individuals, populations and ecosystems using examples from the literature.

Mechanism	Impact	Level of Impact	Effect of impact	Study Organism	References
Restricted Access to Natural Areas/Barriers	Road barriers alter genetic structure between populations.	Populations	**-**	Moose (*Alces alces*); desert bighorn sheep (*Ovis canadensis nelsoni*)	Wilson *et al.* (*48*); Epps *et al.* (*49*)
	Altered animal abundance.	Populations	**-/+**	White-tailed antelope squirrel (*Ammospermophilus leucurus*), black-tailed prairie dog (*Cynomys ludovicianus*), Merriam's kangaroo rat (*Dipodomys merriami*), kangaroo rat (*Dipodomys microps*), prairie vole (*Microtus ochrogaster*), California vole (*Microtus californicus*), house mouse (*Mus musculus*), woodrat (*Notoma lepida*), golden mouse (*Ochrotomys nuttalli*), long-tailed pocket mouse (*Perognathus formosus*), white-footed mouse (*Peromyscus boylii*), white-footed mouse (*Peromyscus leucopus*), deer mouse (*Peromyscus maniculatus*), rat (*Rattus rattus*), eastern chipmunk (*Tamias striatus*), chacoan peccary (*Catagonus wagneri*), European hedgehog (*Erinaceus europaeus*), brown hare (*Lepus europaeus*), American marten (*Martes americana*), European badger (*Meles meles*), koala (*Phascolarctos cinereus*), white-lipped peccary (*Tayassu pecari*), collared peccary (*Tayassu tajacu*), red fox	Fahrig *et al*. (*50*)

				(*Vulpes vulpes*), impala (*Aepyceros melampus*), moose (*Alces alces*), wolf (*Canis lupus*), eastern timber wolf (*Canis lupus lycaon*), black-backed jackal (*Canis mesomelas*), roe deer (*Capreolus capreolus*), elk (*Cervus canadensis*), blue wildebeest (*Connochaetes taurinus*), plains zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis*), African elephant (*Loxondonta africana*), bobcat (*Lynx rufus*), Eurasian lynx (*Lynx lynx*), Iberian lynx (*Lynx pardinus*), mule deer (*Odocoileus hemionus*), Amur tiger (*Panthera tigris altaica*), common warthog (*Phacochoerus africanus*), cougar (*Puma concolor*), woodland caribou (*Rangifer tarandus caribou*), bohor reedbuck (*Redunca redunca*), boar (*Sus scrofa*), eland (*Taurotragus oryx*), brown bear (*Ursus arctos*) and grizzly bear (*Ursus arctos horribilis*).	
	Decreased immigration and colonization success due to barriers.	Populations	-	Animal simulation	Fahrig (*20*)
	Reproduction, body mass and mobility impact susceptibility to roads.	Individual	-/+	Woodland caribou (*Rangifer tarandus*), white-footed mouse (*Peromyscus leucopus*), eastern chipmunk (*Tamias striatus*), hedgehog (*Erinaceus europaeus*), bobcat (*Lynx rufus*), grey wolf (*Canis lupus*), cougar (*Puma concolor*), black bear (*Ursus americanus*), elk (*Cervus elaphus*), moose (*Alces alces*) and grizzly bear (*Ursus arctos*).	Rytwinski *et al.* (*51*)
	Dirt tracks/firebreaks can increase seed dispersal.	Ecosystem	+	Wild boar (*Sus scrofa*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*), red fox (*Vulpes vulpes*),	Suarez-Esteban *et al.* (*52*)

				Eurasian badger (*Meles meles*) and European hare (*Lepus europaeus*).	
	Fragmentation and altered community composition.	Individuals and populations	-	Mammal simulations	Buchmann *et al.* (*53*)
	Tortuosity increases near roads and trails.	Individuals	-	Wolf (*Canis lupus*)	Whittington *et al*. (*54*)
	Small home range and increased overlap near hard boundaries (e.g., roads) and altered genetic composition.	Individuals and populations	-	Coyote (*Canis latrans*) and bobcats (*Lynx rufus*).	Riley *et al.* (*55*)
	Reduced population densities near infrastructure.	Populations	-	Moose (*Alces alces*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), duiker (*Cephalophus* sp), elk (*Cervus canadensis*), blue wildebeest (*Connochaetes taurinus*), Emin's pouched rat (*Cricetomys emini*), link rat (*Deomys ferrugineus*), desert kangaroo rat (*Dipodomys deserti*), plains zebra (*Equus quagga*), red-cheeked rope squirrel (*Funisciurus leucogenys*), shining thicket rat (*Grammomys rutilans*), African dormice (*Graphiurus* sp), African smoky mouse (*Heimyscus fumosus*), Peters' striped mouse (*Hybomys univittatus*), beaded wood mouse (*Hylomyscus* aeta), Allen's wood mouse (*Hylomyscus alleni*), European hare (*Lepus europaeus*), fire-bellied brush-furred rat (*Lophuromys nudicaudus*), African elephant (*Loxodonta africana*), forest elephant (*Loxodonta africana cyclotis*), bobcat (*Lynx rufus*), fawn-footed mosaic-tailed rat (*Melomys cervinipes*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*),	Benitez-Lopez *et al.* (*24*)

				Tullberg's soft-furred mouse (*Praomys tullbergi*), reindeer (*Rangifer tarandus*), rat (*Rattus* spp), round-tailed ground squirrel (*Xerospermophilus tereticaudus*), target rat (*Stochomys longicaudatus*), eland (*Taurotragus* spp), bohor reedbuck (*Redunca redunca*), giant white-tailed rat (*Uromys caudimaculatus*), brown bear (*Ursus arctos*) and black-backed jackal (*Canis mesomelas*).	
	Reduced population densities near infrastructure and restricted movements caused by infrastructure.	Populations	-	Forest elephant (*Loxodonta africana cyclotis*).	Blake *et al.* (*56*)
	Reduced movements due to human settlements/roads and reduced flow of females between populations.	Individuals and populations	-	Grizzly bear (*Ursus arctos*).	Proctor *et al.* (*57*)
Restricted Access AND Increased Resources	Movements tied to artificial water sources and increased recursive movements due to fences, resulting in increased pressure on local resources.	Individuals, populations and ecosystems	-	African elephant (*Loxodonta africana*).	Loarie *et al.* (*58*)
	Smaller home ranges due to supplemental feeding and road barriers.	Individuals and populations	-	Red deer (*Cervus elaphus*)	Jerina *et al.* (*22*)
	Urban resources as an ecological trap: urban sink populations and urban islands impact population genetic structure/flow and increase in conflict with humans due to expanding population numbers.	Individuals and populations	-	Wild boar (*Sus scrofa*)	Stillfried *et al.*(*59*)
	Increased productivity/reproduction, altered migration timing and increased grazing pressure at winter sites due to supplemental feeding, and population declines due to habitat loss.	Individual, population and ecosystem	-/+	Mule deer (*Odocoileus hemionus*)	DeVos *et al.* (*60*); Sandoval *et al.*(*61*); Peterson *et al.*(*62*) ; Bishop *et al.* (*63*).

	Landscape elements (e.g., fruit trees) act as food supplements, allowing populations to persist in fragmented landscapes.	Individuals and populations.	+	Howler monkeys (*Alouatta palliata mexicana*)	Asensio *et al.* (*64*)
Increased Resources (Anthropogenic)	Crop damage leading to human-wildlife conflict.	Individuals and populations	**-**	Wild boars (*Sus scrofa*); Red deer (*Cervus elaphus*).	Honda *et. al.*(*65*)*;* Barrios-Garcia *et al.* (*66*); Bleier et al. (*67*)
	Increase in parasite load and diseases.	Individual and population	**-**	Elk (*Cervus canadensis*); white-tailed deer (*Odocoileus virginianus*).	Hines *et al.*(*68*)*;* Miller *et al*. (*69*): Sorensen *et al.* (*70*)
	Increase group size.	Population	**+**	Arctic fox (*Vulpes lagopus*).	Elmhagen *et al.*(*71*)
	Increased survival rate, increased reproductive rate, improved winter condition, increased hunting, increased population growth rate and reduced density dependence, changed spatial genetic structure, reduced natural selection, increased aggression, increased stress, increased local browsing or grazing, changed plant species composition, invasion of non-native weed species, increased parasitism due to spatial aggregation and increased contact rates and reduced parasitism due to improved body condition.	Individual, population and ecosystem	**-/+**	European bison (*Bison bonasus*), wild boar (*Sus scrofa*), white-tailed deer (*Odocoileus virginianus*), elk (*Cervus canadensis*), and moose (*Alces alces*).	Milner *et al.* (*72*)
	Disruption of movement patterns, circadian rhythm, denning behavior, increased individual interactions, increase population size, culling, increase in diseases, human-animal conflict, alter natural foraging and trophic cascades.	Individual, population and ecosystem	**-/+**	Brown bears (*Ursus arctos*).	Penteriani *et al.*(*73*)
	Consumption of valuable tree	Individual,	**-/+**	European bison (*Bison bonasus*);	Kowalczyk *et*

species, altered social structure, space use and parasites.	population and ecosystem		moose (*Alces alces*).	*al.*(*74*); Mathisen *et al.* (*75*)
Sustain populations in resource poor areas and trophic cascades.	Population and ecosystem	-/+	Dingo (*Canis lupus dingo*).	Newsome *et al.*(*76*, *77*)
Trophic cascades.	Ecosystem	-	African wild dog (*Lycaon pictus*), yellow baboon (*Papio cynocephalus*), black-backed jackal (*Canis mesomelas*), bobcat (*Lynx rufus*), chilla fox (*Pseudalopex griseus*), coyote (*Canis latrans*), culpeo fox (*Pseudalopex culpaeus*), dhole (*Cuon alpinus*), common genet (*Genetta genetta*), Geoffroy's cat (*Oncifelis geoffroyii*), golden jackal (*Canis aureus*), Indian fox (*Vulpes bengalensis*), pampas fox (*Pseudalopex gymnocercus*), red fox (*Vulpes vulpes*) and San Joaquin kit fox (*Vulpes macrotis mutica*), Arabian wolf (*Canis lupus arabs*), black bear (*Ursus americanus*), brown bear (*Ursus arctos*), cheetah (*Acinonyx jubatus*), dingo (*Canis dingo*), Ethiopian wolf (*Canis simensis*), Eurasian lynx (*Lynx lynx*), grey wolf (*Canis lupus*), Mexican grey wolf (*Canis lupus baileyi*), Iberian lynx (*Lynx pardinus*), Iberian wolf (*Canis lupus signatus*), jaguar (*Panthera onca*), leopard (*Panthera pardus*), lion (*Panthera leo*), polar bear (*Ursus maritimus*), puma (*Puma concolor*), snow leopard (*Panthera uncia*), spotted hyena (*Crocuta crocuta*), tiger (*Panthera tigris*); white-tailed deer (*Odocoileus virginianus*); moose (*Alces*	Newsome *et al.*(*78*); Cooper *et al.*(*79*); Gundersen *et al.* (*80*)

				alces).	
	Increase in stress hormones.	Individual	-	Asiatic black bears (*Ursus thibetanus*).	Malcolm *et al.* (*81*)
	Animal-human conflict: death and monetary costs.	Population	-	Brown bear (*Ursus arctos*).	Kavčič *et al.* (*82*)
	Reduced natural selection effects on juveniles.	Individual and population	+	Red deer (*Cervus elaphus*).	Schmidt *et al.* (*83*)
	Reduced and stable home range size due to resources.	Individual	+	Raccoon (*Procyon lotor*); roe deer (*Capreolus capreolus*); red deer (*Cervus elaphus*); Iberian lynx (*Lynx pardinus*).	Prange *et al.*(*5*); Ossi *et al.*(*84*); Lopez-*Bao et al.* (*85*)
	Reduce migration distance and time spent at summer grounds (less quality forage).	Individual	-	Elk (*Cervus canadensis*).	Jones *et al.* (*21*)
	Smaller home range size, covered more distance, nocturnal activity and increase movement speeds.	Individual	+	Wild boar (*Sus scrofa*).	Podgorski *et al.* (*86*)
	Anthropogenic food resources reduce home range size and increases home range overlap, with implications for rabies transmission between individuals.	Individual and populations	-	Indian mongoose (*Herpestes javanicus*).	Quinn *et al.* (*87*)
	Food provisions impact movement behaviors, amplify pathogen invasion due to increased host aggregation and tolerance, but also reduces transmission if provisioned food decreases dietary exposure to parasites.	Individuals and populations	-/+	Elk (*Cervus canadensis*), long-tail macaque (*Macaca fascicularis*), red fox (*Vulpe vulpes*), white-tailed deer (*Odocoileus virginianus*), common vampire bat (*Desmodus rotundus*) and Indian flying fox (*Pteropus giganteus*).	Becker *et al.*(*88*)
	Anthropogenic resources reduce home range size and increases livestock kills by wildlife.	Individuals	-	Spotted hyena (*Crocuta crocuta*).	Kolowski *et al.* (*89*)
	Anthropogenic food reduced core home rage size and increases population size.	Individuals and populations	+	Banded mongoose (*Mungos mungo*).	Gilchrist *et al.* (*23*)

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