

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

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

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

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

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

238 We then calculated displacements as the distance between subsequent GPS locations of
239 each individual at nine time scales (15) ranging from one hour to ten days. For each individual at
240 each time scale, we calculated the 0.5 and the 0.95 quantiles of displacement. The combination of
241 different time scales and quantiles allowed us to examine the effect of the human footprint on
242 both the median (0.5 quantile) and long-distance (0.95 quantile) movements for within-day
243 movements (e.g., 1-hour time scale) up to longer time displacements of over one week (e.g., 10-
244 day time scale). We used linear mixed effects models that, in addition to all covariates (i.e.,

245 NDVI, body mass, diet), also accounted for taxonomy and spatial autocorrelation (see
246 Supplementary Methods for details).

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

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

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

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

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

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

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

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316 **Figures**

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

324
325 **Fig. 2 Mammalian displacement in relation to the Human Footprint Index. (A)** Median and
326 **(B)** long-distance (0.95 quantile) displacements decline with increasing Human Footprint Index
327 at the 10-day scale ($n = 48$ species and 624 individuals). Plots include a smoothing line from a
328 locally weighted polynomial regression. A Human Footprint Index of 0 indicates areas of low
329 human footprint, and a value of 40 represents areas of high human footprint.

330
331 **Fig. 3 Model coefficients (\pm CI) of linear mixed effects models predicting mammalian**
332 **displacements using the (A) Human Footprint Index (HFI), (B) Normalized Difference**
333 **Vegetation Index (NDVI), and (C) body mass.** Models were run for the median (blue) and
334 long-distance (0.95 quantiles; red) displacements of each individual calculated across different
335 time scales. When the error bars cross the horizontal line the effect is not significant. See
336 Supplementary Tables S3 for details.

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406

407 **Acknowledgements** Funding was provided by the Robert Bosch Foundation and additional
408 funding sources (see Supplementary Text). The data reported in this paper are available at
409 datadryad.org (doi:xxx). M.A.T., T.M., K.B.-G., W.F.F., J.M.F., and B.M conceived the
410 manuscript, M.A.T. and T.M. conducted the analyses and wrote the first manuscript draft. Co-
411 authors contributed data sets and assisted with writing the final version of the manuscript.

412

413 **Supplementary Materials:**

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Supplementary Materials for

Moving in the Anthropocene: Global Reductions in Terrestrial Mammalian Movements

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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* (1, 2) and *Loxodonta africana* (3, 4)), 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 (5). 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 (6). 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 $\pm 4\%$ (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 ($> 4 \text{ m s}^{-1}$), and removed them (7). 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 (8) (HFI; Supplementary Table S2). NDVI data was extracted from MODIS Land Terra Vegetation Indices 500-m 16-day resolution (MOD13A1 V005 (9)) using the Movebank Env-DATA system (10) (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 (11) (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 (12) 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 (13, 14). All model predictions and associated standard errors were calculated using the “AICcmodavg” R package (15). All analyses were performed in R version 3.2.2 (16).

Supplementary Text

Extended List of Acknowledgements

The authors are grateful for support from the Robert Bosch Foundation, Goethe International Postdoctoral Programme, People Programme (Marie Curie Actions) of the European Union's Seventh Framework Programme FP7/2007-2013/ under REA grant agreement no [291776], German Research Foundation (DFG, FR 3246/2-1), US National Science Foundation (NSF) ABI-1458748, NSF grant #0963022, NSF grant #1255913, Irish Research Council GOIPD/2015/81, NASA funded project: "Animals on the Move", grant NNX15AV92, Research Council of Norway (Grant number 251112), GLOBE POL-NOR/198352/85/2013, UC Berkeley Museum of Vertebrate Zoology, American Society of Mammalogists, NSF DEB-LTREB Grant # 1556248, NSF DDIG grant 0608467, NASA Earth Science Division, Ecological Forecasting Program project number NNX11AP61G, NSF Biological Infrastructure Award #1564380, German Research Foundation (DFG) AOBJ 576687, ANR FEAR, ANR SAVARID, Leverhulme Study Abroad Studentship and ERC (323401), Copenhagen Zoo, the Danish Environmental Protection Agency, 15. Juni Charity Foundation, DFG Research Training Group 2118/1 BioMove, Grant SFRH/BPD/111084/2015 from Fundação para a Ciência e Tecnologia, the “MOVEIT” ANR grant ANR-16 -CE02-0010-02, Save the Elephants, Spanish Ministry of Economy and Competitiveness (grant number IJCI-2014-19190), NSF grants (BCS 99-03949 and BCS 1266389), the L.S.B. Leakey Foundation, and the University of California, Davis, Committee on 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. Keeseey) (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. Puma, maned wolf and lynx silhouettes by M. Tucker.

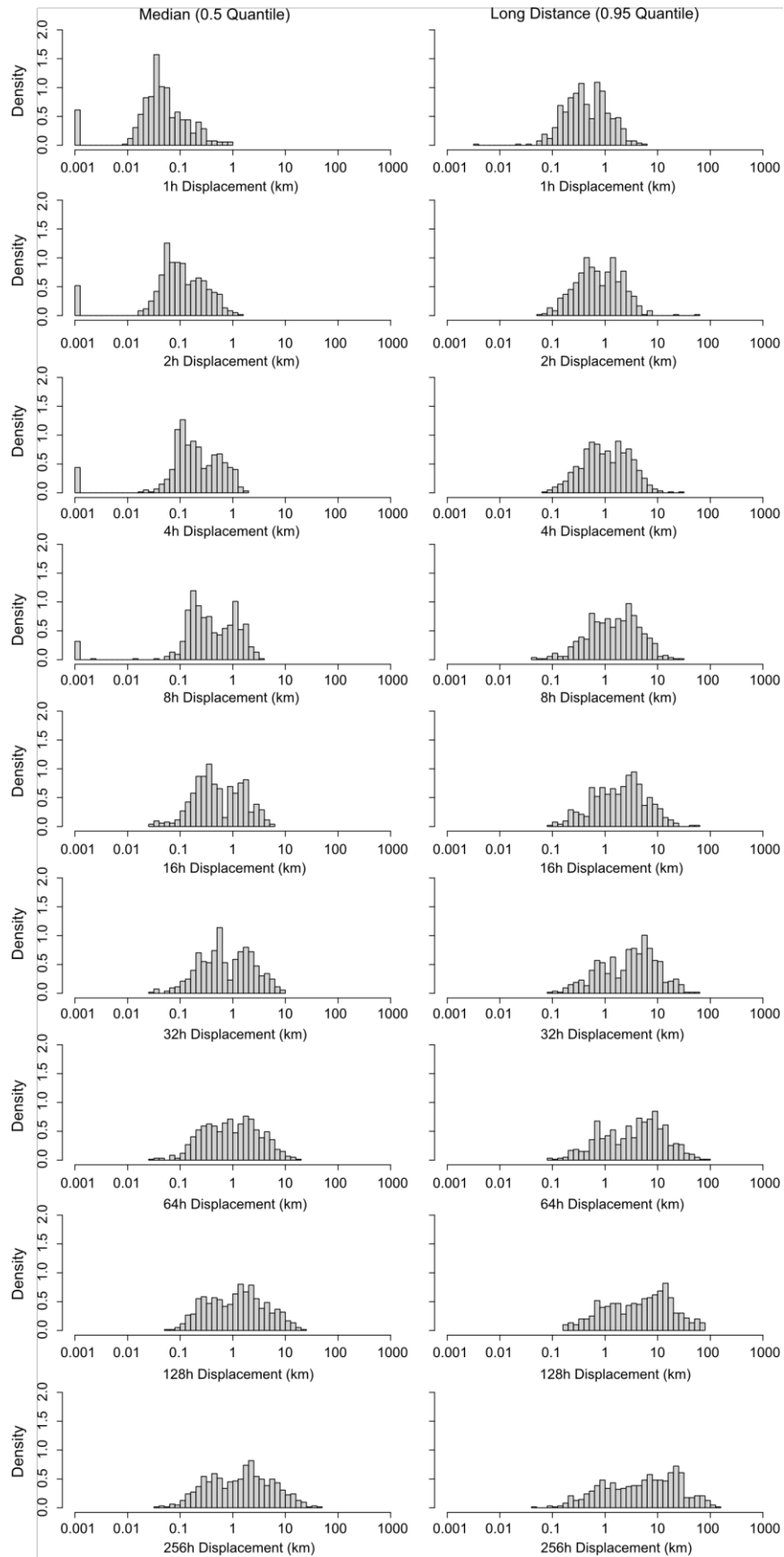


Fig. S1.

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.

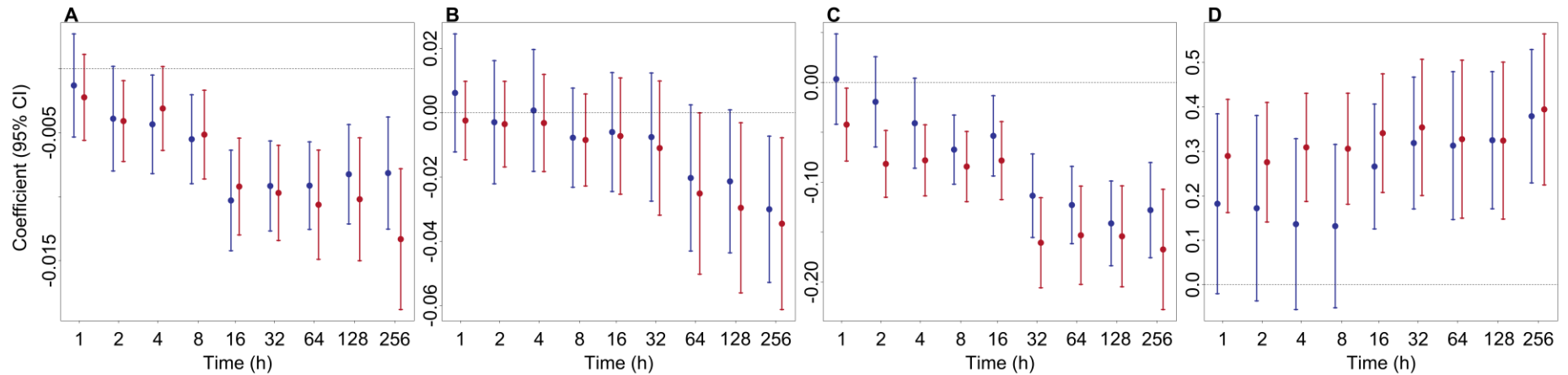


Fig. S2

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 (8, 17)	Log ₁₀
Body Mass	Grams	Not applicable.	Not applicable.	K. E. Jones <i>et al.</i> , PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. <i>Ecology</i> . 90 , 2648 (2009).	Log ₁₀
Diet	Unitless, categorical	Not applicable.	Not applicable.	K. E. Jones <i>et al.</i> , PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. <i>Ecology</i> . 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
<i>Aepyceros melampus</i>	20	Co-author	<i>Madoqua guentheri</i>	15	Co-author
<i>Alces alces</i>	46	Co-author	<i>Martes pennanti</i>	13	Movebank
<i>Antilocapra americana</i>	25	Co-author	<i>Myrmecophaga tridactyla</i>	4	Co-author
<i>Beatragus hunteri</i>	4	Co-author	<i>Odocoileus hemionus</i>	25	Co-author
<i>Canis aureus</i>	1	Movebank	<i>Odocoileus hemionus columbianus</i>	14	Co-author
<i>Canis latrans</i>	19	Movebank	<i>Odocoileus virginianus</i>	30	Movebank
<i>Canis lupus</i>	12	Co-author & Movebank	<i>Ovibos moschatus</i>	14	Co-author
<i>Capreolus capreolus</i>	94	Eurodeer & co-author	<i>Panthera leo</i>	2	Movebank
<i>Cercocebus galeritus*</i>	1	Co-author	<i>Panthera onca</i>	4	Co-author
<i>Cerdocyon thous</i>	10	Co-author	<i>Panthera pardus</i>	4	Movebank
<i>Cervus elaphus</i>	47	Co-author, Eurodeer & Movebank	<i>Papio anubis</i>	4	Movebank
<i>Chlorocebus pygerythrus</i>	12	Movebank	<i>Papio cynocephalus*</i>	22	Co-author & Movebank
<i>Chrysocyon brachyurus</i>	12	Movebank	<i>Procapra gutturosa</i>	15	Co-author
<i>Connochaetes taurinus</i>	3	Co-author	<i>Procyon lotor</i>	9	Movebank
<i>Dasyopus novemcinctus</i>	1	Co-author	<i>Propithecus verreauxi*</i>	28	Co-author
<i>Elephas maximus</i>	2	Movebank	<i>Puma concolor</i>	6	Co-author
<i>Equus grevyi</i>	7	Movebank	<i>Rangifer tarandus</i>	14	Co-author
<i>Equus hemionus</i>	6	Co-author	<i>Saguinus geoffroyi*</i>	3	Movebank
<i>Equus quagga</i>	27	Co-author & Movebank	<i>Saiga tatarica</i>	3	Co-author
<i>Eulemur rufifrons</i>	4	Co-author	<i>Sus scrofa</i>	26	Co-author
<i>Euphractus sexcinctus</i>	7	Co-author	<i>Syncerus caffer</i>	6	Movebank
<i>Felis silvestris</i>	5	Movebank	<i>Tamandua mexicana</i>	2	Movebank
<i>Giraffa camelopardalis</i>	5	Co-author	<i>Tapirus terrestris</i>	4	Co-author
<i>Gulo gulo</i>	5	Co-author	<i>Tolypeutes matacus</i>	5	Co-author
<i>Lepus europaeus</i>	39	Movebank	<i>Trichosurus vulpecula*</i>	29	Co-author
<i>Loxodonta africana</i>	14	Co-author & Movebank	<i>Ursus americanus</i>	21	Movebank
<i>Loxodonta africana cyclotis</i>	23	Movebank	<i>Ursus arctos</i>	13	Co-author
<i>Lynx lynx</i>	6	Co-author	<i>Vulpes vulpes</i>	5	Movebank
<i>Lynx rufus</i>	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 (18). 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	0.096	0.288***	0.138	0.268***	0.105	0.297***	0.126	0.288***	0.195*	0.301***	0.265***	0.325***	0.33***	0.321***	0.336***	0.306**	0.423***	0.403***
NDVI	0.004	-0.041*	-0.019	-0.081***	-0.04	-0.078***	-0.067***	-0.086***	-0.056**	-0.078***	-0.115***	-0.161***	-0.124***	-0.155***	-0.144***	-0.158***	-0.132***	-0.172***
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)	0.225	-0.209	0.175	-0.172	-0.018	-0.363	-0.026	-0.431	-0.342	-0.497*	-0.552*	-0.598*	-0.72**	-0.527	-0.558*	-0.342	-0.638*	-0.46
Diet (O)	0.185	-0.127	0.052	-0.066	-0.006	-0.186	0.073	-0.233	-0.123	-0.248	-0.307	-0.403	-0.494	-0.445	-0.45*	-0.346	-0.492*	-0.398
r² Marginal	0.034	0.286	0.045	0.255	0.016	0.346	0.022	0.35	0.228	0.415	0.349	0.443	0.406	0.347	0.391	0.28	0.459	0.381
r² Conditional	0.922	0.865	0.932	0.895	0.958	0.887	0.977	0.901	0.875	0.885	0.898	0.898	0.906	0.87	0.871	0.846	0.866	0.835
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 (18). 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	0.129	0.287***	0.143	0.267***	0.127***	0.292	0.116	0.268***	0.203*	0.301***	0.254**	0.301***	0.271**	0.236*	0.279**	0.218*	0.373***	0.33***
NDVI	0.003	-0.041*	-0.019	-0.08***	-0.041	-0.077***	-0.067***	-0.085***	-0.056*	-0.078***	-0.115**	-0.16***	-0.122**	-0.152*	-0.142**	-0.154*	-0.127***	-0.166***
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	0.005	-0.002	-0.003	-0.004	0.001	-0.005	-0.008	-0.01	-0.008	-0.009	-0.011	-0.015	-0.022	-0.031	-0.025	-0.036*	-0.031*	-0.038*
Diet (H)	0.206	-0.209	0.168	-0.172	-0.023	-0.36	-0.035	-0.421	-0.352	-0.497*	-0.544*	-0.571*	-0.626*	-0.46	-0.477	-0.304	-0.66**	-0.42
Diet (O)	0.169	-0.126	0.047	-0.066	-0.018	-0.185	0.068	-0.233	-0.131	-0.249	-0.301	-0.383	-0.424	-0.384	-0.381	-0.288	-0.499*	-0.356
r^2 Marginal	0.037	0.282	0.045	0.252	0.016	0.342	0.023	0.345	0.222	0.407	0.343	0.433	0.394	0.367	0.406	0.323	0.528	0.428
r^2 Conditional	0.921	0.866	0.932	0.896	0.958	0.889	0.978	0.905	0.874	0.886	0.901	0.902	0.913	0.886	0.884	0.87	0.882	0.853
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 (<i>Alces alces</i>); desert bighorn sheep (<i>Ovis canadensis nelsoni</i>)	Wilson <i>et al.</i> (19); Epps <i>et al.</i> (20)
	Altered animal abundance.	Populations	-/+	White-tailed antelope squirrel (<i>Ammospermophilus leucurus</i>), black-tailed prairie dog (<i>Cynomys ludovicianus</i>), Merriam's kangaroo rat (<i>Dipodomys merriami</i>), kangaroo rat (<i>Dipodomys microps</i>), prairie vole (<i>Microtus ochrogaster</i>), California vole (<i>Microtus californicus</i>), house mouse (<i>Mus musculus</i>), woodrat (<i>Notoma lepida</i>), golden mouse (<i>Ochrotomys nuttalli</i>), long-tailed pocket mouse (<i>Perognathus formosus</i>), white-footed mouse (<i>Peromyscus boylii</i>), white-footed mouse (<i>Peromyscus leucopus</i>), deer mouse (<i>Peromyscus maniculatus</i>), rat (<i>Rattus rattus</i>), eastern chipmunk (<i>Tamias striatus</i>), chacoan peccary (<i>Catagonus wagneri</i>), hedgehog (<i>Erinaceus europaeus</i>), brown hare (<i>Lepus europaeus</i>), American marten (<i>Martes americana</i>), badger (<i>Meles meles</i>), koala (<i>Phascolarctos cinereus</i>), white-lipped peccary (<i>Tayassu pecari</i>), collared peccary (<i>Tayassu tajacu</i>), red fox (<i>Vulpes vulpes</i>), Impala (<i>Aepyceros</i>)	Fahrig <i>et al.</i> (21)

				<i>melampus</i>), moose (<i>Alces alces</i>), wolf (<i>Canis lupus</i>), eastern timber wolf (<i>Canis lupus lycaon</i>), black-backed jackal (<i>Canis mesomelas</i>), roe deer (<i>Capreolus capreolus</i>), elk (<i>Cervus canadensis</i>), wildebeest (<i>Connochaetes taurinus</i>), zebra (<i>Equus quagga</i>), giraffe (<i>Giraffa camelopardalis</i>), African elephant (<i>Loxodonta africana</i>), bobcat (<i>Lynx rufus</i>), Eurasian lynx (<i>Lynx lynx</i>), Iberian lynx (<i>Lynx pardinus</i>), mule deer (<i>Odocoileus hemionus</i>), Amur tiger (<i>Panthera tigris altaica</i>), warthog (<i>Phacochoerus africanus</i>), cougar (<i>Puma concolor</i>), woodland caribou (<i>Rangifer tarandus caribou</i>), bohor reedbuck (<i>Redunca redunca</i>), boar (<i>Sus scrofa</i>), eland (<i>Taurotragus oryx</i>), brown bear (<i>Ursus arctos</i>) and grizzly bear (<i>Ursus arctos horribilis</i>).	
	Decreased immigration and colonization success due to barriers.	Populations	-	Animal simulation	Fahrig (22)
	Reproduction, body mass and mobility impact susceptibility to roads.	Individual	-/+	Woodland caribou (<i>Rangifer tarandus</i>), white-footed mouse (<i>Peromyscus leucopus</i>), eastern chipmunk (<i>Tamias striatus</i>), hedgehog (<i>Erinaceus europaeus</i>), bobcat (<i>Lynx rufus</i>), grey wolf (<i>Canis lupus</i>), cougar (<i>Puma concolor</i>), black bear (<i>Ursus americanus</i>), elk (<i>Cervus elaphus</i>), moose (<i>Alces alces</i>) and grizzly bear (<i>Ursus arctos</i>).	Rytwinski <i>et al.</i> (23)
	Dirt tracks/firebreaks can increase seed dispersal.	Ecosystem	+	Wild boar (<i>Sus scrofa</i>), red deer (<i>Cervus elaphus</i>), fallow deer (<i>Dama dama</i>), red fox (<i>Vulpes vulpes</i>), Eurasian badger (<i>Meles meles</i>) and	Suarez-Esteban <i>et al.</i> (24)

				European hare (<i>Lepus europaeus</i>).	
	Fragmentation and altered community composition.	Individuals and populations	-	Mammal simulations	Buchmann <i>et al.</i> (25)
	Tortuosity increases near roads and trails.	Individuals	-	Wolf (<i>Canis lupus</i>)	Whittington <i>et al.</i> (26)
	Small home range and increased overlap near hard boundaries (e.g., roads) and altered genetic composition.	Individuals and populations	-	Coyote (<i>Canis latrans</i>) and bobcats (<i>Lynx rufus</i>).	Riley <i>et al.</i> (27)
	Reduced population densities near infrastructure.	Populations	-	Moose (<i>Alces alces</i>), coyote (<i>Canis latrans</i>), red fox (<i>Vulpes vulpes</i>), duiker (<i>Cephalophus</i> sp), elk (<i>Cervus canadensis</i>), blue wildebeest (<i>Connochaetes taurinus</i>), Emin's pouched rat (<i>Cricetomys emini</i>), link rat (<i>Deomys ferrugineus</i>), desert kangaroo rat (<i>Dipodomys deserti</i>), plains zebra (<i>Equus quagga</i>), red-cheeked rope squirrel (<i>Funisciurus leucogenys</i>), shining thicket rat (<i>Grammomys rutilans</i>), African dormice (<i>Graphiurus</i> sp), African smoky mouse (<i>Heimyscus fumosus</i>), Peters' striped mouse (<i>Hybomys univittatus</i>), beaded wood mouse (<i>Hylomyscus aeta</i>), Allen's wood mouse (<i>Hylomyscus alleni</i>), European hare (<i>Lepus europaeus</i>), fire-bellied brush-furred rat (<i>Lophuromys nudicaudus</i>), African elephant (<i>Loxodonta africana</i>), forest elephant (<i>Loxodonta africana cyclotis</i>), bobcat (<i>Lynx rufus</i>), fawn-footed mosaic-tailed rat (<i>Melomys cervinipes</i>), mule deer (<i>Odocoileus hemionus</i>), white-tailed deer (<i>Odocoileus virginianus</i>), Tullberg's soft-furred mouse (<i>Praomys</i>	Benitez-Lopez <i>et al.</i> (28)

				<i>tullbergi</i>), reindeer (<i>Rangifer tarandus</i>), rat (<i>Rattus</i> spp), round-tailed ground squirrel (<i>Spermophilus tereticaudus</i>), target rat (<i>Stochomys longicaudatus</i>), eland (<i>Taurotragus</i> spp), bohor reedbuck (<i>Redunca redunca</i>), giant white-tailed rat (<i>Uromys caudimaculatus</i>), brown bear (<i>Ursus arctos</i>) and black-backed jackal (<i>Canis mesomelas</i>).	
	Reduced population densities near infrastructure and restricted movements caused by infrastructure.	Populations	-	Forest elephants (<i>Loxodonta africana cyclotis</i>).	Blake <i>et al.</i> (29)
	Reduced movements due to human settlements/roads and reduced flow of females between populations.	Individuals and populations	-	Grizzly bears (<i>Ursus arctos</i>).	Proctor <i>et al.</i> (30)
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 (<i>Loxodonta africana</i>).	Loarie <i>et al.</i> (31)
	Smaller home ranges due to supplemental feeding and road barriers.	Individuals and populations	-	Red deer (<i>Cervus elaphus</i>)	Jerina <i>et al.</i> (32)
	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 (<i>Sus scrofa</i>)	Stillfried <i>et al.</i> (33)
	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 (<i>Odocoileus hemionus</i>)	DeVos <i>et al.</i> (34); Sandoval <i>et al.</i> (35); Peterson <i>et al.</i> (36) ; Bishop <i>et al.</i> (37).

	Landscape elements (e.g., fruit trees) act as food supplements, allowing populations to persist in fragmented landscapes.	Individuals and populations.	+	Howler monkeys (<i>Alouatta palliata mexicana</i>)	Asensio <i>et al.</i> (38)
Increased Resources (Anthropogenic)	Crop damage leading to human-wildlife conflict.	Individuals and populations	-	Wild boars (<i>Sus scrofa</i>); Red deer (<i>Cervus elaphus</i>).	Honda <i>et al.</i> (39); Barrios-Garcia <i>et al.</i> (40); Bleier <i>et al.</i> (41)
	Increase in parasite load and diseases.	Individual and population	-	Elk (<i>Cervus canadensis</i>); white-tailed deer (<i>Odocoileus virginianus</i>).	Hines <i>et al.</i> (42); Miller <i>et al.</i> (43); Sorensen <i>et al.</i> (44)
	Increase group size.	Population	+	Arctic fox (<i>Vulpes lagopus</i>).	Elmhagen <i>et al.</i> (45)
	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 (<i>Bison bonasus</i>), wild boar (<i>Sus scrofa</i>), white-tailed deer (<i>Odocoileus virginianus</i>), elk (<i>Cervus canadensis</i>) and moose (<i>Alces alces</i>).	Milner <i>et al.</i> (46)
	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 (<i>Ursus arctos</i>).	Penteriani <i>et al.</i> (47)
	Consumption of valuable tree species, altered social structure, space	Individual, population and	-/+	European bison (<i>Bison bonasus</i>); moose (<i>Alces alces</i>).	Kowalczyk <i>et al.</i> (48); Mathisen <i>et</i>

use and parasites.	ecosystem			<i>al. (49)</i>
Sustain populations in resource poor areas and trophic cascades.	Population and ecosystem	-/+	Dingo (<i>Canis lupus dingo</i>).	Newsome <i>et al.</i> (50, 51)
Trophic cascades.	Ecosystem	-	African wild dog (<i>Lycaon pictus</i>), yellow baboon (<i>Papio cynocephalus</i>), black-backed jackal (<i>Canis mesomelas</i>), bobcat (<i>Lynx rufus</i>), chilla fox (<i>Pseudalopex griseus</i>), coyote (<i>Canis latrans</i>), culpeo fox (<i>Pseudalopex culpaeus</i>), dhole (<i>Cuon alpinus</i>), common genet (<i>Genetta genetta</i>), Geoffroy's cat (<i>Oncifelis geoffroyii</i>), golden jackal (<i>Canis aureus</i>), Indian fox (<i>Vulpes bengalensis</i>), pampas fox (<i>Pseudalopex gymnocercus</i>), red fox (<i>Vulpes vulpes</i>) and San Joaquin kit fox (<i>Vulpes macrotis mutica</i>), Arabian wolf (<i>Canis lupus arabs</i>), black bear (<i>Ursus americanus</i>), brown bear (<i>Ursus arctos</i>), cheetah (<i>Acinonyx jubatus</i>), dingo (<i>Canis dingo</i>), Ethiopian wolf (<i>Canis simensis</i>), Eurasian lynx (<i>Lynx lynx</i>), grey wolf (<i>Canis lupus</i>), Mexican grey wolf (<i>Canis lupus baileyi</i>), Iberian lynx (<i>Lynx pardinus</i>), Iberian wolf (<i>Canis lupus signatus</i>), jaguar (<i>Panthera onca</i>), leopard (<i>Panthera pardus</i>), lion (<i>Panthera leo</i>), polar bear (<i>Ursus maritimus</i>), puma (<i>Puma concolor</i>), snow leopard (<i>Panthera uncia</i>), spotted hyena (<i>Crocuta crocuta</i>), tiger (<i>Panthera tigris</i>); white-tailed deer (<i>Odocoileus virginianus</i>); moose (<i>Alces alces</i>).	Newsome <i>et al.</i> (52); Cooper <i>et al.</i> (53); Gundersen <i>et al.</i> (54)

Increase in stress hormones.	Individual	-	Asiatic black bears (<i>Ursus thibetanus</i>).	Malcolm <i>et al.</i> (55)
Animal-human conflict: death and monetary costs.	Population	-	Brown bear (<i>Ursus arctos</i>).	Kavčič <i>et al.</i> (56)
Reduced natural selection effects on juveniles.	Individual and population	+	Red deer (<i>Cervus elaphus</i>).	Schmidt <i>et al.</i> (57)
Reduced and stable home range size due to resources.	Individual	+	Racoon (<i>Procyon lotor</i>) ; Roe deer (<i>Capreolus capreolus</i>) ; Red deer (<i>Cervus elaphus</i>); Iberian lynx (<i>Lynx pardinus</i>).	Prange <i>et al.</i> (58); Ossi <i>et al.</i> (59); Lopez-Bao <i>et al.</i> (60)
Reduce migration distance and time spent at summer grounds (less quality forage).	Individual	-	Elk (<i>Cervus canadensis</i>).	Jones <i>et al.</i> (61)
Smaller home range size, covered more distance, nocturnal activity and increase movement speeds.	Individual	+	Wild boar (<i>Sus scrofa</i>).	Podgorski <i>et al.</i> (62)
Anthropogenic food resources reduce home range size and increases home range overlap, with implications for rabies transmission between individuals.	Individual and populations	-	Indian mongoose (<i>Herpestes javanicus</i>).	Quinn <i>et al.</i> (63)
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 (<i>Cervus canadensis</i>), long-tail macaque (<i>Macaca fascicularis</i>) , red fox (<i>Vulpe vulpes</i>), white-tailed deer (<i>Odocoileus virginianus</i>), common vampire bat (<i>Desmodus rotundus</i>) and flying fox (<i>Pteropus giganteus</i>).	Becker <i>et al.</i> (64)
Anthropogenic resources reduce home range size and increases livestock kills by wildlife.	Individuals	-	Spotted hyena (<i>Crocuta crocuta</i>).	Kolowski <i>et al.</i> (65)
Anthropogenic food reduced core home range size and increases population size.	Individuals and populations	+	Banded mongoose (<i>Mungos mungo</i>).	Gilchrist <i>et al.</i> (66)

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