

HUMAN IMPACTS

Moving in the Anthropocene: Global reductions in terrestrial mammalian movements

Marlee A. Tucker,^{1,2*} Katrin Böhning-Gaese,^{1,2} William F. Fagan,^{3,4} John M. Fryxell,⁵ Bram Van Moorter,⁶ Susan C. Alberts,⁷ Abdullahi H. Ali,⁸ Andrew M. Allen,^{9,10} Nina Attias,¹¹ Tal Avgar,¹² Hattie Bartlam-Brooks,¹³ Buuveibaatar Bayarbaatar,¹⁴ Jerrold L. Belant,¹⁵ Alessandra Bertassoni,¹⁶ Dean Beyer,¹⁷ Laura Bidner,¹⁸ Floris M. van Beest,¹⁹ Stephen Blake,^{20,21} Niels Blaum,²² Chloe Bracis,^{1,2} Danielle Brown,²³ P. J. Nico de Bruyn,²⁴ Francesca Cagnacci,^{25,26} Justin M. Calabrese,^{3,27} Constança Camilo-Alves,^{28,29} Simon Chamailé-Jammes,³⁰ Andre Chiaradia,^{31,32} Sarah C. Davidson,^{33,20} Todd Dennis,³⁴ Stephen DeStefano,³⁵ Duane Diefenbach,³⁶ Iain Douglas-Hamilton,^{37,38} Julian Fennessy,³⁹ Claudia Fichtel,⁴⁰ Wolfgang Fiedler,²⁰ Christina Fischer,⁴¹ Ilya Fischhoff,⁴² Christen H. Fleming,^{3,27} Adam T. Ford,⁴³ Susanne A. Fritz,^{1,2} Benedikt Gehr,⁴⁴ Jacob R. Goheen,⁴⁵ Eliezer Gurarie,^{3,46} Mark Hebblewhite,⁴⁷ Marco Heurich,^{48,49} A. J. Mark Hewison,⁵⁰ Christian Hof,¹ Edward Hurme,³ Lynne A. Isbell,^{18,51} René Janssen,⁵² Florian Jeltsch,²² Petra Kaczensky,^{6,53} Adam Kane,⁵⁴ Peter M. Kappeler,⁴⁰ Matthew Kauffman,⁵⁵ Roland Kays,^{56,57} Duncan Kimuyu,⁵⁸ Flavia Koch,^{40,59} Bart Kranstauber,⁴⁴ Scott LaPoint,^{20,60} Peter Leimgruber,²⁷ John D. C. Linnell,⁶ Pascual López-López,⁶¹ A. Catherine Markham,⁶² Jenny Mattison,⁶ Emilia Patricia Medici,^{63,64} Ugo Mellone,⁶⁵ Evelyn Merrill,¹² Guilherme de Miranda Mourão,⁶⁶ Ronaldo G. Morato,⁶⁷ Nicolas Morellet,⁵⁰ Thomas A. Morrison,⁶⁸ Samuel L. Díaz-Muñoz,^{69,70} Atle Mysterud,⁷¹ Dejid Nandintsetseg,^{1,2} Ran Nathan,⁷² Aidin Niamir,¹ John Odden,⁷³ Robert B. O'Hara,^{1,74} Luiz Gustavo R. Oliveira-Santos,⁷⁵ Kirk A. Olson,¹⁴ Bruce D. Patterson,⁷⁶ Rogerio Cunha de Paula,⁶⁷ Luca Pedrotti,⁷⁷ Björn Reineking,^{78,79} Martin Rimmer,⁸⁰ Tracey L. Rogers,⁸¹ Christer Moe Rolandsen,⁶ Christopher S. Rosenberry,⁸² Daniel I. Rubenstein,⁸³ Kamran Safi,^{20,84} Sonia Saïd,⁸⁵ Nir Sapir,⁸⁶ Hall Sawyer,⁸⁷ Niels Martin Schmidt,^{19,88} Nuria Selva,⁸⁹ Agnieszka Sergiel,⁸⁹ Enkhtuvshin Shiilegdamba,¹⁴ João Paulo Silva,^{90,91,92} Navinder Singh,⁹ Erling J. Solberg,⁶ Orr Spiegel,⁹³ Olav Strand,⁶ Siva Sundaresan,⁹⁴ Wiebke Ullmann,²² Ulrich Voigt,⁹⁵ Jake Wall,³⁷ David Wattles,³⁵ Martin Wikelski,^{20,84} Christopher C. Wilmers,⁹⁶ John W. Wilson,⁹⁷ George Wittemyer,^{37,98} Filip Zięba,⁹⁹ Tomasz Zwijacz-Kozica,⁹⁹ Thomas Mueller^{1,2,27*}

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 movements of mammals in areas with a comparatively high human footprint were on average one-half to one-third the extent of their movements in areas with a low human footprint. We attribute this reduction to behavioral changes of individual animals and to 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 affects not only population persistence but also ecosystem processes such as predator-prey interactions, nutrient cycling, and disease transmission.

With approximately 50 to 70% of 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 not only is causing the loss of habitat and biodiversity, but is also affecting how animals move through fragmented and disturbed habitats. The extent to which animal movements are affected by anthropogenic effects on the structure and composition of landscapes and resource changes has been explored only in

local geographic regions or within single species. Such studies typically report decreasing animal movements—for example, as a result of 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).

We conducted a global comparative study of how the human footprint affects movements of terrestrial nonvolant 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 ($n = 28, 11, \text{ and } 18$ 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, nighttime lights, railways, roads, and navigable waterways (9) (see supplementary materials 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. Because individuals may need to cover a larger area to gather sufficient resources, mammals generally move farther in environments with lower productivity (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 both herbivores and carnivores (11). Because an allometric scaling relationship shows that animals of greater body size usually move farther (12), and because diet may influence movements as a result of differences in foraging costs and availability of resource types (13, 14), 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 1 hour to 10 days. For each individual at each time scale, we calculated the 0.5 and 0.95 quantile of displacement. The combination of different time scales and quantile 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 more than 1 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 materials for details).

We found strong negative effects of the human footprint on median and long-distance displacements of terrestrial mammals (Fig. 2, Fig. 3A, and table S3). Displacements of individuals (across species) living in areas of high footprint (HFI = 36) were shorter than displacements of individuals living in areas of low footprint (HFI = 0) by as much as a factor of 3. For example, median displacements for carnivores over 10 days were 3.3 ± 1.4 km (SE) in areas of high footprint versus 6.9 ± 1.3 km in areas of low footprint (Fig. 2A and table S3). Likewise, the maximum displacement distances for carnivores at the 10-day scale averaged 6.6 ± 1.4 km in areas of high footprint versus 21.5 ± 1.4 km in areas of low footprint (Fig. 2B and table S3). The effect was significant on all temporal scales with 8 hours or more between locations.

The effect was not significant at shorter time scales (Fig. 3A, 1 to 4 hours), which suggests 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 attributable to (i) an individual-behavioral effect, where individuals alter their movements relative to the human footprint, or (ii) 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: (i) 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 (ii) 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 quantile) at most time scales (from 8 hours to 10 days) (fig. S2A and table S4). The species occurrence effect was significant only over longer time scales (128- and

256-hour periods, or 5 and 10 days, respectively) (fig. S2B and 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 traveled farther than smaller species (Fig. 3C and tables S3 and S4). Second, we found a negative

¹Senckenberg Biodiversity and Climate Research Centre, Senckenberg Gesellschaft für Naturforschung, 60325 Frankfurt (Main), Germany. ²Department of Biological Sciences, Goethe University, 60438 Frankfurt (Main), Germany. ³Department of Biology, University of Maryland, College Park, MD 20742, USA. ⁴SESYNC, University of Maryland, Annapolis, MD 21401, USA. ⁵Department of Integrative Biology, University of Guelph, Guelph, Ontario N1G 2W1, Canada. ⁶Norwegian Institute for Nature Research, P.O. Box 5685 Torgard, NO-7485 Trondheim, Norway. ⁷Departments of Biology and Evolutionary Anthropology, Duke University, Durham, NC 27708, USA. ⁸Hiroa Conservation Programme, Garissa, Kenya. ⁹Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, Umeå 90183, Sweden. ¹⁰Institute for Water and Wetland Research, Department of Animal Ecology and Physiology, Radboud University, 6500GL Nijmegen, Netherlands. ¹¹Ecology and Conservation Graduate Program, Federal University of Mato Grosso do Sul, Campo Grande, MS, Brazil. ¹²Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada. ¹³Structure and Motion Laboratory, Royal Veterinary College, University of London, London NW1 0TU, UK. ¹⁴Wildlife Conservation Society, Mongolia Program, Ulaanbaatar, Mongolia. ¹⁵Carnivore Ecology Laboratory, Forest and Wildlife Research Center, Mississippi State University, Box 9690, Mississippi State, MS, USA. ¹⁶Animal Biology Postgraduate Program, São Paulo State University, São José do Rio Preto, SP 15054-000, Brazil. ¹⁷Michigan Department of Natural Resources, 1990 U.S. 41 South, Marquette, MI 49855, USA. ¹⁸Department of Anthropology, University of California, Davis, CA 95616, USA. ¹⁹Department of Bioscience, Aarhus University, 4000 Roskilde, Denmark. ²⁰Max Planck Institute for Ornithology, Vogelwarte Radolfzell, D-78315 Radolfzell, Germany. ²¹Wildlife Conservation Society, Bronx, NY 10460, USA. ²²University of Potsdam, Plant Ecology and Nature Conservation, 14476 Potsdam, Germany. ²³Department of Biology, Middle Tennessee State University, Murfreesboro, TN 37132, USA. ²⁴Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Hatfield 0028, Gauteng, South Africa. ²⁵Department of Biodiversity and Molecular Ecology, Research and Innovation Centre, Fondazione Edmund Mach, 38010 San Michele all'Adige (TN), Italy. ²⁶Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA. ²⁷Smithsonian Conservation Biology Institute, National Zoological Park, Front Royal, VA, USA. ²⁸Departamento de Fitotecnia, Universidade de Évora, Pólo da Mitra, 7002-554 Évora, Portugal. ²⁹ICAAM-Institute of Mediterranean Agricultural and Environmental Sciences, University of Évora, Évora, Portugal. ³⁰Centre d'Ecologie Fonctionnelle et Evolutive UMR 5175, CNRS-Université de Montpellier-Université Paul-Valéry Montpellier-EPHE, 34293 Montpellier Cedex 5, France. ³¹Phillip Island Nature Parks, Victoria, Australia. ³²School of Biological Sciences, Monash University, Melbourne, Australia. ³³Department of Civil, Environmental and Geodetic Engineering, Ohio State University, Columbus, OH 43210, USA. ³⁴Department of Biology, Fiji National University, P.O. Box 5529, Natabua, Lautoka, Fiji Islands. ³⁵U.S. Geological Survey, Massachusetts Cooperative Fish and Wildlife Research Unit, University of Massachusetts, Amherst, MA 01003, USA. ³⁶U.S. Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State University, University Park, PA 16802, USA. ³⁷Save the Elephants, P.O. Box 54667, Nairobi 00200, Kenya. ³⁸Department of Zoology, University of Oxford, Oxford OX1 3PS, UK. ³⁹Giraffe Conservation Foundation, P.O. Box 86099, Eros, Namibia. ⁴⁰German Primate Center, Behavioral Ecology and Sociobiology Unit, 37077 Göttingen, Germany. ⁴¹Restoration Ecology, Department of Ecology and Ecosystem Management, Technische Universität München, 85354 Freising, Germany. ⁴²Cary Institute of Ecosystem Studies, Millbrook, NY 12545, USA. ⁴³Irving K. Barber School of Arts and Sciences, Unit 2: Biology, University of British Columbia, Okanagan Campus, Kelowna, BC V1V 1V7, Canada. ⁴⁴Department of Evolutionary Biology and Environmental Studies, University of Zurich, 8057 Zurich, Switzerland. ⁴⁵Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA. ⁴⁶School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195, USA. ⁴⁷Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA. ⁴⁸Bavarian Forest National Park, Department of Conservation and Research, 94481 Grafenau, Germany. ⁴⁹Chair of Wildlife Ecology and Management, Albert Ludwigs University of Freiburg, 79106 Freiburg, Germany. ⁵⁰CEFS, Université de Toulouse, INRA, Castanet Tolosan, France. ⁵¹Animal Behavior Graduate Group, University of California, Davis, CA 95616, USA. ⁵²Bionet Natuuronderzoek, 6171EL Stein, Netherlands. ⁵³Research Institute of Wildlife Ecology, University of Veterinary Medicine Vienna, A-1160 Vienna, Austria. ⁵⁴School of Biological, Earth and Environmental Sciences, University College Cork, Cork, Ireland. ⁵⁵U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY, USA. ⁵⁶North Carolina Museum of Natural Sciences, Raleigh, NC 27601, USA. ⁵⁷Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA. ⁵⁸Department of Natural Resource Management, Karatina University, P.O. Box 1957-10101, Karatina, Kenya. ⁵⁹Department of Psychology, University of Lethbridge, Lethbridge, Alberta T1K 3M4, Canada. ⁶⁰Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY 10964, USA. ⁶¹Cavanilles Institute of Biodiversity and Evolutionary Biology, Terrestrial Vertebrates Group, University of Valencia, E-46980 Paterna, Valencia, Spain. ⁶²Department of Anthropology, Stony Brook University, Stony Brook, NY 11794, USA. ⁶³International Union for Conservation of Nature (IUCN) Species Survival Commission (SSC) Tapir Specialist Group (TSG), Rua Licuala, 622, Damha 1, Campo Grande, CEP: 79046-150, Mato Grosso do Sul, Brazil. ⁶⁴IPÊ (Instituto de Pesquisas Ecológicas; Institute for Ecological Research), Caixa Postal 47, Nazaré Paulista, CEP: 12960-000, São Paulo, Brazil. ⁶⁵Vertebrates Zoology Research Group, Departamento de Ciencias Ambientales y Recursos Naturales, University of Alicante, Alicante, Spain. ⁶⁶Embrapa Pantanal, Corumbá, MS 79320-900, Brazil. ⁶⁷National Research Center for Carnivores Conservation, Chico Mendes Institute for the Conservation of Biodiversity, Atibaia-SP 12952-011, Brazil. ⁶⁸Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, UK. ⁶⁹Center for Genomics and Systems Biology, Department of Biology, New York University, New York, NY 10003, USA. ⁷⁰Department of Microbiology and Molecular Genetics, University of California, Davis, CA 95616, USA. ⁷¹Centre for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo, Blindern, NO-0316 Oslo, Norway. ⁷²Movement Ecology Laboratory, Department of Ecology, Evolution and Behavior, Alexander Silberman Institute of Life Sciences, Hebrew University of Jerusalem, Jerusalem 91904, Israel. ⁷³Norwegian Institute for Nature Research, NO-0349 Oslo, Norway. ⁷⁴Department of Mathematical Sciences and Centre for Biodiversity Dynamics, Norwegian University of Science and Technology (NTNU), 7491 Trondheim, Norway. ⁷⁵Department of Ecology, Federal University of Mato Grosso do Sul, Campo Grande, MS 79070-900, Brazil. ⁷⁶Integrative Research Center, Field Museum of Natural History, Chicago, IL 60605, USA. ⁷⁷Consorzio Parco Nazionale dello Stelvio, Bormio (Sondrio), Italy. ⁷⁸Univ. Grenoble Alpes, Irstea, UR LESSEM, BP 76, 38402 St-Martin-d'Hères, France. ⁷⁹University of Bayreuth, BayCEER, 95447 Bayreuth, Germany. ⁸⁰Nationalpark Schwarzwald, 77889 Seebach, Germany. ⁸¹Evolution and Ecology Research Centre and School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia. ⁸²Pennsylvania Game Commission, Harrisburg, PA 17110, USA. ⁸³Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA. ⁸⁴Department of Biology, University of Konstanz, 78467 Konstanz, Germany. ⁸⁵Directorate of Studies and Expertise (DRE), Office National de la Chasse et de la Faune Sauvage, Montfort, 01330 Birieux, France. ⁸⁶Department of Evolutionary and Environmental Biology, University of Haifa, 3498838 Haifa, Israel. ⁸⁷Western Ecosystems Technology Inc., Laramie, WY 82070, USA. ⁸⁸Arctic Research Centre, Aarhus University, 8000 Aarhus C, Denmark. ⁸⁹Institute of Nature Conservation Polish Academy of Sciences, 31-120 Krakow, Poland. ⁹⁰REN Biodiversity Chair, CIBIO/InBIO Associate Laboratory, Universidade do Porto, Campus Agrário de Vairão, 4485-661 Vairão, Portugal. ⁹¹Centre for Applied Ecology "Prof. Baeta Neves"/InBIO Associate Laboratory, Instituto Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisbon, Portugal. ⁹²Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências da Universidade de Lisboa, Campo Grande, 1749-016 Lisbon, Portugal. ⁹³Department of Environmental Science and Policy, University of California, Davis, CA, USA. ⁹⁴Jackson Hole Conservation Alliance, Jackson, WY 83001, USA. ⁹⁵Institute for Terrestrial and Aquatic Wildlife Research, University of Veterinary Medicine Hannover-Foundation, 30173 Hannover, Germany. ⁹⁶Center for Integrated Spatial Research, Environmental Studies Department, University of California, Santa Cruz, CA 95060, USA. ⁹⁷Department of Zoology and Entomology, University of Pretoria, Hatfield 0028, South Africa. ⁹⁸Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, CO 80523, USA. ⁹⁹Tatra National Park, 34-500 Zakopane, Poland.

*Corresponding author. Email: tucker.marlee@gmail.com (M.A.T.); thomas.mueller@senckenberg.de (T.M.)

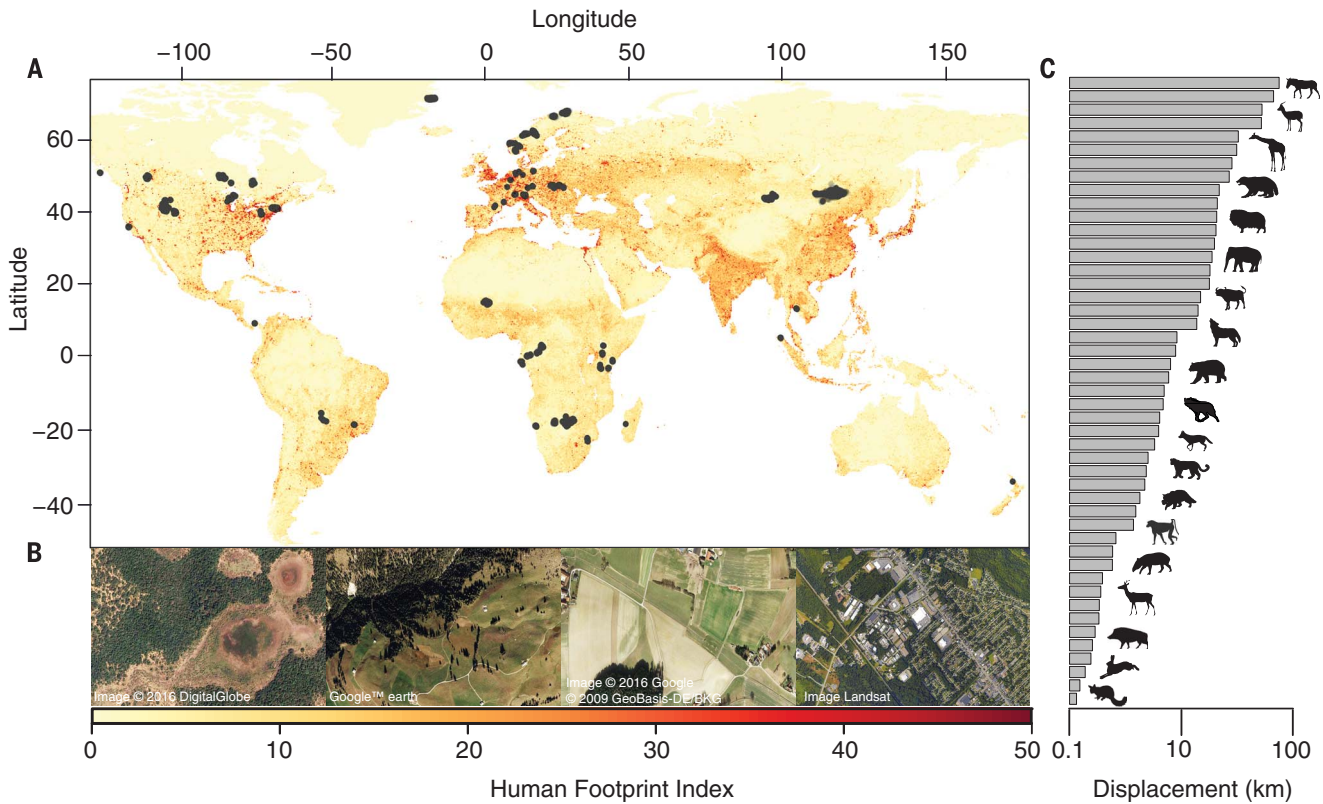


Fig. 1. Locations from the GPS tracking database and the Human Footprint Index. (A) GPS relocations of 803 individuals across 57 species plotted on the global map of the Human Footprint Index (HFI) spanning from 0 (low; yellow) to 50 (high; red). (B) Examples of landscapes under HFI = 2 (the Pantanal,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

gazelle (*Procapra gutturosa*), giraffe (*Giraffa camelopardalis*), wolverine (*Gulo gulo*), muskox (*Ovibos moschatus*), African forest elephant (*Loxodonta africana cyclotis*), African buffalo (*Syncerus caffer*), wolf (*Canis lupus*), brown bear (*Ursus arctos*), maned wolf (*Chrysocyon brachyurus*), coyote (*Canis latrans*), leopard (*Panthera pardus*), wildcat (*Felis silvestris*), yellow baboon (*Papio cynocephalus*), tapir (*Tapirus terrestris*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), European hare (*Lepus europaeus*), brushtail possum (*Trichosurus vulpecula*).

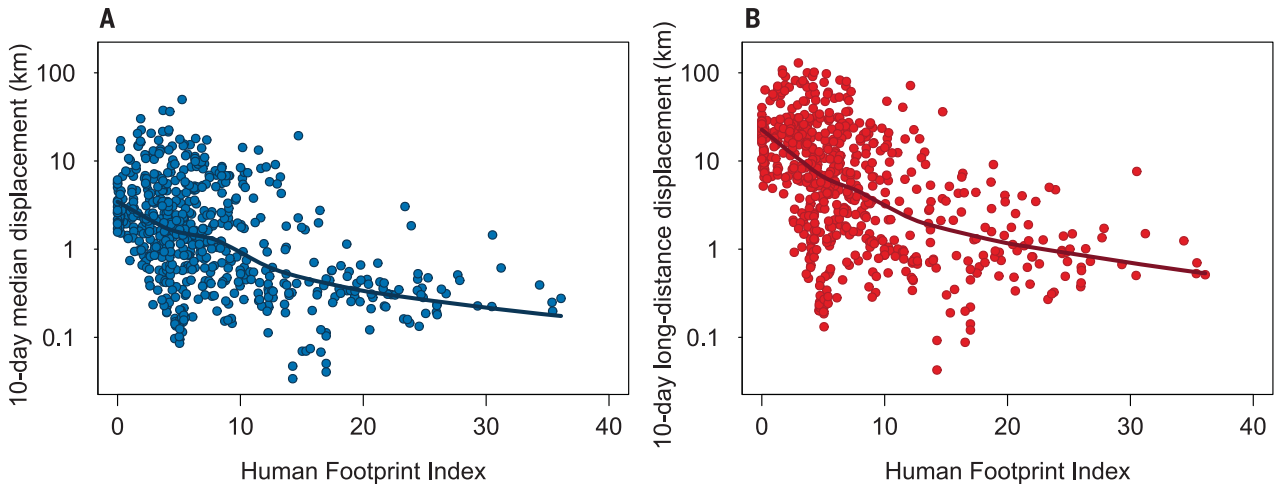


Fig. 2. Mammalian displacement in relation to the Human Footprint Index. (A) Median displacements; (B) long-distance (0.95 quantile) displacements. Both displacements decline with increasing HFI at the 10-day scale ($n = 48$ species and 624 individuals). Plots include a smoothing line from a locally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

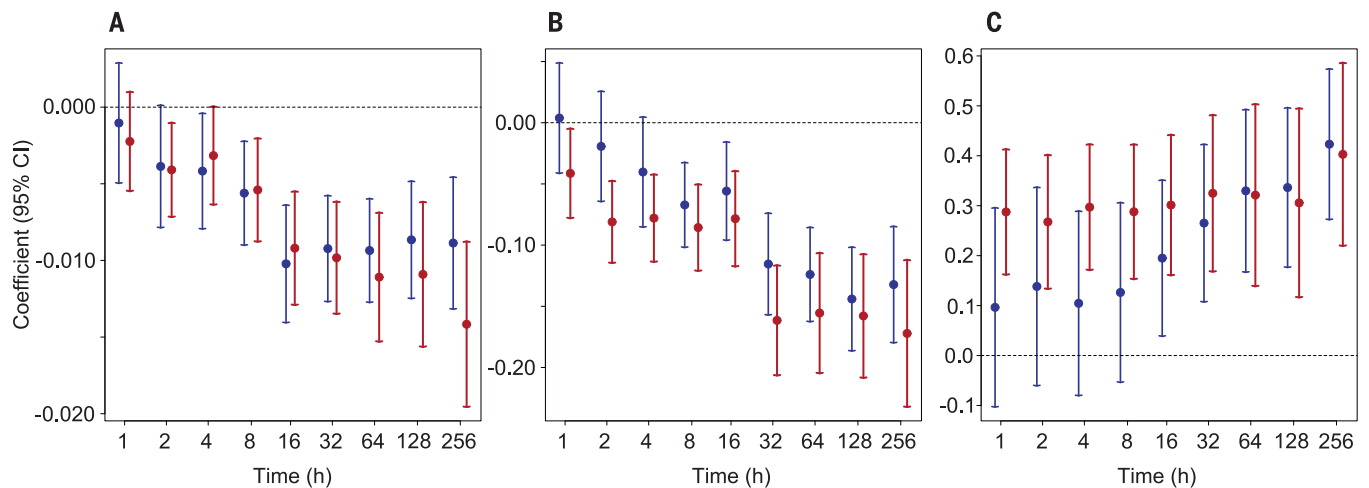


Fig. 3. Model coefficients (with confidence intervals) of linear mixed-effects models predicting mammalian displacements. Coefficient values are shown for (A) Human Footprint Index (HFI), (B) Normalized Difference Vegetation Index (NDVI), and (C) body mass.

Models were run for the median (blue) and long-distance (0.95 quantile; red) displacements of each individual calculated across different time scales. Where the error bars cross the horizontal line, the effect is not significant. See table S3 for details.

relationship between resource availability and displacement distance, such that movements were on average shorter in environments with higher resources (Fig. 3B and tables 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 traveled on average farther per unit time than herbivores and omnivores (tables 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 8 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: (i) movement barriers such as habitat change and fragmentation (19, 20) and (ii) reduced movement requirements attributable 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 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 because of the enhancement of resources via supplemental feeding and the disturbance and fragmentation caused by the presence of roads (22).

Although 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 affect ecosystems regardless of the underlying mechanisms and go far beyond the focal individuals themselves. Animal move-

ments are essential for ecosystem functioning because 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 strive to maintain landscape permeability by including animal movement as a key conservation metric. Ultimately, because of the critical role of animal movement in human/wildlife coexistence (29) and disease spread (30), the effects of reduced vagility may go beyond ecosystem functioning to directly affect human well-being.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
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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, Buuveibaatar Bayarbaatar, Jerrold L. Belant, Alessandra Bertassoni, Dean Beyer, Laura Bidner, Floris M. van Beest, Stephen Blake, Niels Blaum, Chloe Bracis, Danielle Brown, P. J. Nico de Bruyn, Francesca Cagnacci, Justin M. Calabrese, Constança Camilo-Alves, Simon Chamailé-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 M. 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. Diaz-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 Rimpler, 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 Zieba, Tomasz Zwijacz-Kozica and Thomas Mueller

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Restrictions on roaming

Until the past century or so, the movement of wild animals was relatively unrestricted, and their travels contributed substantially to ecological processes. As humans have increasingly altered natural habitats, natural animal movements have been restricted. Tucker *et al.* examined GPS locations for more than 50 species. In general, animal movements were shorter in areas with high human impact, likely owing to changed behaviors and physical limitations. Besides affecting the species themselves, such changes could have wider effects by limiting the movement of nutrients and altering ecological interactions.

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