Moving in the Anthropocene: Global reductions in terrestrial mammalian movements

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Abstract

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).

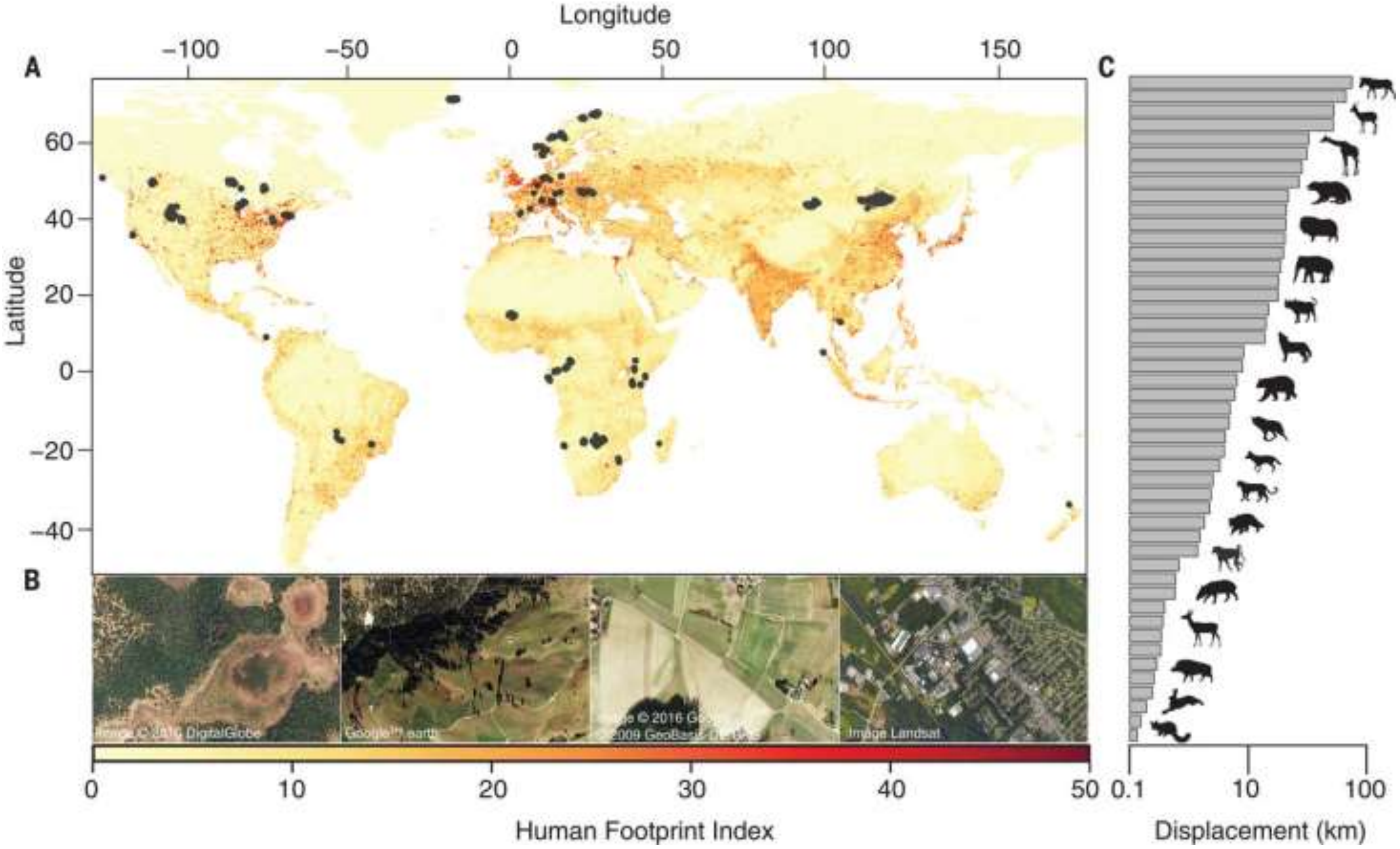

Fig. 1 Locations from the GPS tracking database and the Human Footprint Index.

(**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*).

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.

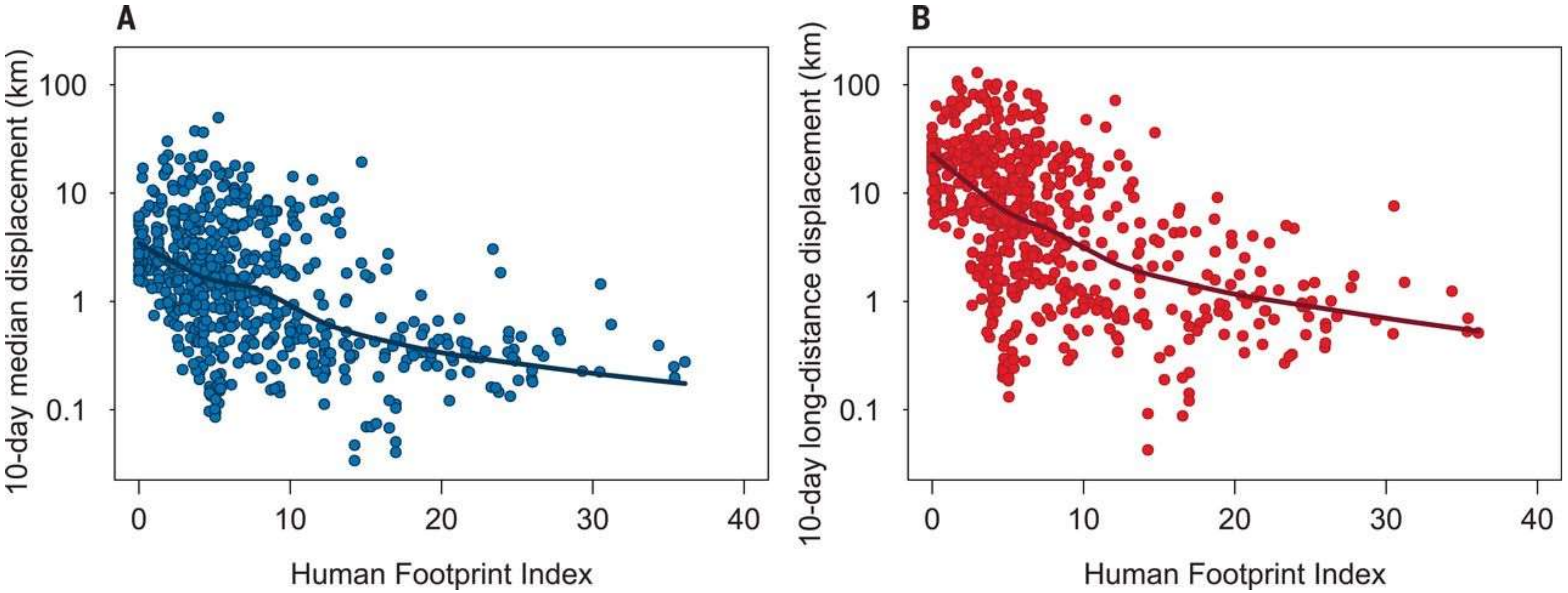

Fig. 2 Mammalian displacement in relation to the Human Footprint Index.

(**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.

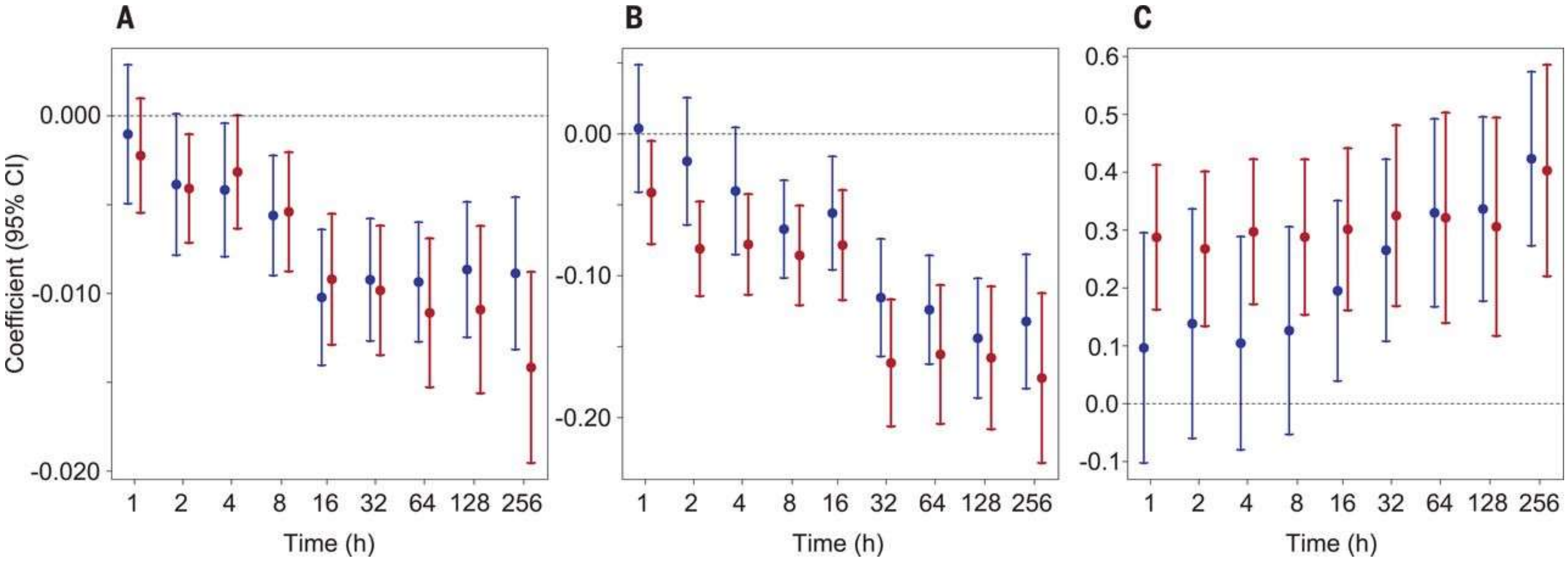

Fig. 3 Model coefficients (with confidence intervals) of linear mixed-effects models predicting mammalian displacements.

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.

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 & 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.

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Supplementary Materials:

Materials and Methods
Supplementary Text
Figures S1-S2
Tables S1-S5
References (*31-94*)