

Current Biology

Human footprint and protected areas shape elephant range across Africa

Highlights

- 229 African elephants were tracked across forest, Sahel, savanna, and bushveld sites
- Protected areas and the human footprint both constrain elephant range size
- 62% of the African continent is potential elephant habitat, of which elephants use 17%
- 85% of potential elephant habitat lies outside current protected areas

Authors

Jake Wall, George Wittemyer, Brian Klinkenberg, ..., Fiona Maisels, Jelle Ferwerda, Iain Douglas-Hamilton

Correspondence

jake@maraelephantproject.org

In brief

Using GPS tracking from 229 African elephants across Sahel, forest, savannah, and bushveld sites, Wall et al. show that protected areas and the human footprint are the main factors affecting elephant range size. A habitat suitability model shows that 62% of Africa is potentially habitable, but elephants occupy just 17% of the 18 million square kilometers.



Report

Human footprint and protected areas shape elephant range across Africa

Jake Wall,^{1,2,16,*} George Wittemyer,^{2,3} Brian Klinkenberg,⁴ Valerie LeMay,⁵ Stephen Blake,^{6,7,8,9} Samantha Strindberg,⁶ Michelle Henley,^{10,11} Fritz Vollrath,^{3,12,13} Fiona Maisels,^{6,14} Jelle Ferwerda,¹⁵ and Iain Douglas-Hamilton^{3,12}

¹Mara Elephant Project, PO Box 2606, Nairobi, Kenya, 00502

²Department of Fish, Wildlife and Conservation Biology, Colorado State University, 1474 Campus Delivery, Fort Collins, CO 80523, USA

³Save the Elephants, PO Box 54667, Nairobi, Kenya, 00200

⁴Lab for Advanced Spatial Analysis, Department of Geography, University of British Columbia, 1984 West Mall, Vancouver B.C., Canada, V6T 1Z2

⁵Department of Forest Resources Management, Faculty of Forestry, University of British Columbia, Forest Sciences Centre #2045–2424 Main Mall, Vancouver, B.C., Canada, V6T 1Z4

⁶Global Conservation Program, Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460, USA

⁷Max Planck Institute of Animal Behavior, Am Obstberg 1, 78315 Radolfzell, Germany

⁸Biology Department, Saint Louis University, Biology Extension Building, 1008 S. Spring Ave. St. Louis, MO 63103, USA

⁹WildCare Institute, Saint Louis Zoo, 1 Government Drive, Saint Louis, MO 63100, USA

¹⁰Applied Behavioural Ecology and Ecosystem Research Unit, School of Environmental Sciences, University of South Africa, Private Bag X5, Florida 1710, South Africa

¹¹Elephants Alive, PO Box 960, Hoedspruit 1380, South Africa

¹²Department of Zoology, Oxford University, Oxford OX1 3PS, UK

¹³Mpala Research Centre, PO Box 555 - 10400, Nanyuki, Kenya

¹⁴School of Natural Sciences, University of Stirling, FK9 4LA, Scotland, United Kingdom

¹⁵University of Twente, Faculty of Engineering Technology, PO Box 217, 7500 AE Enschede, the Netherlands

¹⁶Lead contact

*Correspondence: jake@maraelephantproject.org

<https://doi.org/10.1016/j.cub.2021.03.042>

SUMMARY

Over the last two millennia, and at an accelerating pace, the African elephant (*Loxodonta spp.* Lin.) has been threatened^{1–7} by human activities across its range. We investigate the correlates of elephant home range sizes across diverse biomes. Annual and 16-day elliptical time density home ranges⁸ were calculated by using GPS tracking data collected from 229 African savannah and forest elephants (*L. africana* and *L. cyclotis*, respectively) between 1998 and 2013 at 19 sites representing bushveld, savannah, Sahel, and forest biomes. Our analysis considered the relationship between home range area and sex, species, vegetation productivity, tree cover, surface temperature, rainfall, water, slope, aggregate human influence, and protected area use. Irrespective of these environmental conditions, long-term annual ranges were overwhelmingly affected by human influence and protected area use. Only over shorter, 16-day periods did environmental factors, particularly water availability and vegetation productivity, become important in explaining space use. Our work highlights the degree to which the human footprint and existing protected areas now constrain the distribution of the world's largest terrestrial mammal.^{9,10} A habitat suitability model, created by evaluating every square kilometer of Africa, predicts that 18,169,219 km² would be suitable as elephant habitat—62% of the continent. The current elephant distribution covers just 17% of this potential range of which 57.4% falls outside protected areas. To stem the continued extirpation and to secure the elephants' future, effective and expanded protected areas and improved capacity for coexistence across unprotected range are essential.

RESULTS

African elephants have suffered major decreases in their geographic range and numbers across most of the continent because of continued killing for ivory, habitat loss, and the growth of human populations and their associated pressures.^{1–7} African savannah elephants (*Loxodonta africana*) and African forest elephants (*Loxodonta cyclotis*) can live in most ecosystems in Africa, from semi-deserts to tropical swamp forests and from lowlands to montane habitats. Elephants typically have large ranges that

exceed protected area boundaries.^{11–13} Many elephant populations inhabit regions that are undergoing rapid anthropogenic change, such as increases in logging, roads, agriculture, pastoralism, charcoal extraction, degradation of pristine areas, and compression of elephants into protected areas. These changes might often result in increased human–elephant conflict.¹⁴ Understanding elephant space use and the drivers of ranging patterns is critical to future conservation and land use planning efforts.

In this study, we examined the correlates of the home ranges of 229 individual elephants across Africa. Using data collected at



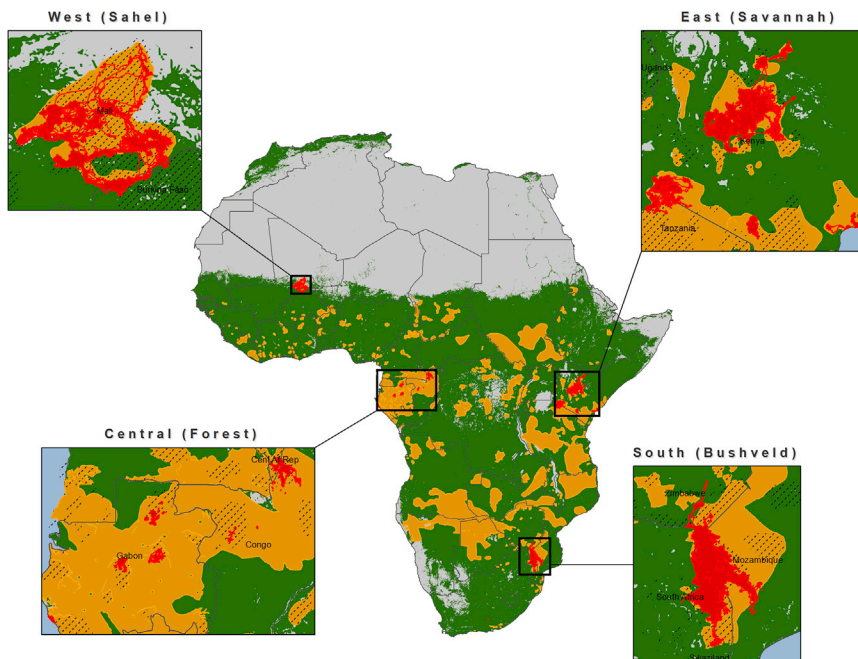


Figure 1. A habitat suitability model for elephants

From the range of conditions encountered by the tracked elephants over 16-day periods, an HSM was extrapolated to each kilometer square grid of Africa (shown in green). Currently, 18,169,219 km² is suitable range for elephants, which is 62% of the whole continent but for extreme deserts, cities, and high mountain tops. Of the HSM, 85% falls outside of protected areas. It was the likely range of elephants two millennia before the present. The current elephant range (orange) is 3,132,238 km², according to the African Elephant Specialist Group,⁵ of which 57% falls outside of protected areas. The combined elliptical time-density 90th percentile ranges (red), of our sample of 229 collared elephants is 72,113 km². The protected area boundaries (black hatched areas on the inset maps) are from the World Database on Protected Areas (WDPA).¹⁵

19 sites across the 4 primary biomes located in Africa—Sahel (west), forest (central), savannah (east), and bushveld (south)—we relate space use to sex, species, and remotely sensed environmental and anthropogenic variables. We asked three questions about continental ranging patterns of African elephants. Question 1: how do elephant home ranges vary in size across sexes, species, and biome? Question 2: how influential are (i) individual (sex and species); (ii) biotic (vegetation productivity and tree cover); (iii) abiotic (surface temperature, rainfall, water, and slope); and (iv) anthropogenic (aggregate human influence and protected area use) factors on elephant range size? Question 3: how much suitable elephant habitat remains across Africa and how much of this suitable habitat is currently occupied?

Elliptical time-density (ETD)⁸ 90th percentile range areas were calculated at 19 sites, representing the major biomes where African elephants are found (Figure 1). The area covered by these combined individual ranges was 72,113 km², approximately 2.1% of the current, estimated total continental range of African elephants (i.e., ‘Known’ + ‘Possible’ = 3,366,405 km²).⁵ A total of 31% (22,289 km²) of measured individual ranges fell outside of protected areas, primarily in East and West Africa.

In answer to question 1 (how do elephant home ranges vary in size across sexes, species, and biome?), male elephant annual ranges (median = 189.6 km², interquartile range (IQR) = 112.5–288.8 km²) were larger than for females (median = 153.0 km², IQR = 108.4–255.1 km²); however, 16-day female ranges (median = 19.9 km², IQR = 11.7–32.6 km²) were marginally larger than for males (median = 18.4 km², IQR = 10.2–34.5 km²). Between species, savannah elephants had larger annual (median = 172.9 km², IQR = 112.8–281.0 km²) ranges than did forest elephants (median = 64.6 km², IQR = 25.2–131.3 km²), and also had larger 16-day ranges (median = 19.3 km², IQR = 11.0–33.5 km²) than did forest elephants (median = 11.1 km², IQR = 6.5–18.7 km²). Across biomes, in order of decreasing

range size, annual ranges followed this pattern: Sahel (median = 426.8 km², IQR = 319.1–586.7 km²), bushveld (me-

di-
dian = 231.4 km², IQR = 157.6–350.6 km²), savannah (median = 125.8 km², IQR = 84.4–206.9 km²), and then forest (median = 64.6 km², IQR = 25.2–131.3 km²). Sixteen-day elephant range sizes followed a similar pattern: Sahel (median = 25.1 km², IQR = 14.2–45.4 km²), bushveld (median = 24.6 km², IQR = 13.6–45.6 km²), savannah (median = 16.4 km², IQR = 9.7–27.2 km²), and finally forest (median = 11.1 km², IQR = 6.51–18.70 km²).

The single largest annual ETD range was 1,130.3 km² (a male in Kruger, South Africa). The single smallest annual ETD range was 8.4 km² (a female in Loango, Gabon). The single largest 16-day ETD range was 598 km² (a male in Gourma, Mali); the single smallest 16-day ETD range was 0.16 km² (a male in Laikipia, Kenya).

Our top models of 16-day and annual ranges, based on the Corrected Akaike’s Information Criterion (AICc)^{16,17} weights (Table 1), designed to address question 2 (how influential are individual, biotic, abiotic, and anthropogenic factors on elephant range size?), demonstrated that factors influencing space-use differed across these two temporal scales. At annual timescales, only individual and anthropogenic factors were retained in the final model (Table 1; Figure 2). The top annual range model had an AICc weight of 0.829 compared with that of the next highest ranked model, which had a weight of 0.124 (Table 1). Range size decreased with increasing protected area intersection (PAI) and human footprint index (HFI) (Figure 2). Range sizes of *L. cyclotis* were again smaller than those of *L. africana* and annual ranges of males were larger than those of females (Table S6).

In contrast, the top 16-day range model included all individual, biotic, abiotic, and anthropogenic factors except sex (Table 1). This model had an AICc weight of 0.604 compared with 0.221 for the next highest AICc-ranked model (Table 1), and the only difference between the top two models being the exclusion of the sex parameter, demonstrating 16-day ranges were not significantly affected by the sex of the animal. Range size increased with higher values of permanent water intersection (WATER),

Table 1. Annual and 16-day model selection

| Timescale | Model name | Specification | AICc | delta | weight |
|-----------|---------------------------------|--|----------|-------|--------|
| annual | m_anthro_indv | LOG(RANGE) ~SPECIES + PAI + HFI + SEX | 373.8 | 0.00 | 0.829 |
| annual | m_anthro | LOG(RANGE) ~PAI + HFI | 377.6 | 3.80 | 0.124 |
| annual | m_full | LOG(RANGE) ~SPECIES + PAI + HFI + SEX + NDWI + TRMM + NDVI + SLOPE + WATER | 380.5 | 6.64 | 0.030 |
| 16-day | m_biotic_abiotic_anthro_species | LOG(RANGE) ~SPECIES + WATER + PAI + NDVI + HFI + LST + SLOPE + TRMM + TREE | 18,662.5 | 0.00 | 0.604 |
| 16-day | m_full | LOG(RANGE) ~SPECIES + WATER + PAI + NDVI + HFI + LST + SLOPE + TRMM + SEX + TREE | 18,664.5 | 2.01 | 0.221 |
| 16-day | m_biotic_abiotic_anthro_sex | LOG(RANGE) ~WATER + PAI + NDVI + HFI + LST + SLOPE + TRMM + TREE + SEX | 18,665.0 | 2.49 | 0.174 |

Model selection table showing the top three models defining competing hypotheses of the relationship between log-transformed annual and 16-day elephant range areas and environmental, anthropogenic, and endogenous covariates. The top selected annual model (m_anthro_indv) contains only anthropogenic, sex, and species covariates, whereas the top selected 16-day model (m_biotic_abiotic_anthro_species) contains abiotic, biotic, anthropogenic, and species covariates (coefficient values presented in Table S6).

normalized difference vegetation index (NDVI), land surface temperature (LST), and tropical rainfall monitoring mission estimated precipitation rates (TRMM), whereas it decreased with increasing PAI, HFI, topographic slope (SLOPE), and percent tree cover (TREE) (Figure 3; Table S6). Model outputs also showed that range sizes of *L. cyclotis* were smaller than those of *L. africana* (Figure 3; Table S6), as summarized above.

To answer question 3, (how much suitable elephant habitat remains across Africa and how much of this suitable habitat is currently occupied?), we calculated the min-max range of covariate values encountered by any subject within the 16-day ranges across the continent (Table S5) and used these as inputs in an elephant habitat suitability model (HSM) (Figure 1). The HSM predicts a potential elephant distribution of 18,169,219 km² (i.e., 62% of the African land mass). The habitats suitable for elephants cover almost the whole of Africa, with the exception of extreme habitats such as the Sahara, Danakil, Kalahari, and Namib deserts; cities; towns; and high mountain tops. Of the HSM area, just 17.2% is occupied by the African Elephant Specialist Group of the International Union for Conservation of Nature's (IUCN) map of "known and possible ranges."

DISCUSSION

Here, we provide a trans-continental comparative analysis of elephant ranging behavior on the basis of GPS tracking data across a diversity of habitats, from rainforest to savannahs, and arid semi-deserts in Africa, covering nearly the full range of conditions experienced by savannah and forest elephants. By assessing covariates thought to drive movements, across 19 distinct sites and hundreds of individuals, this study provides a comprehensive assessment for African elephants of their current space-use. Our analysis was made possible by the advent of the global scale remote-sensing Google Earth Engine platform²⁸ combined with our own custom analysis tools²⁹ (www.movementecology.net) to calculate elephant ranges over multiple temporal scales and link each range area with a series of remotely sensed covariates.

Sex, species, and site variation in elephant range size

African elephants show a high-degree of sexual dimorphism (males 5/3 the size of females) and differing sexually based social

behaviors; females move in family units, focus on rearing young, and tend to take fewer risks than more solitary males who also move further during their musth period.^{30,31} These differences in size and sociality can manifest as markedly different foraging and spatial strategies,^{32,33} which our analysis shows in sex-based differences in annual elephant range sizes (Figure 2; Table S6). However, over shorter 16-day durations, sex differences in ranging area were not apparent (Figure 3; Table S6).

In addition to sexual differences, elephants are highly individual in their space-use,^{11,34} as represented by the high contribution of the individual ID random effects to the overall variance. Despite such variation, forest elephants had overall smaller ranges than savannah elephants. This difference likely reflects less need to move far in the more productive forest biome. In addition, frugivory is common and highly nutritious.^{35,36} Greater productivity, or more specific knowledge of fruiting tree locations, and the seasonal nature of fruiting appears to drive more focused space-use among forest elephants.

Biotic, abiotic, and anthropogenic drivers of range size

We found that two anthropogenic factors—human footprint and protected area intersection—were dominant in explaining annual range sizes. These covariates were also instrumental in models of 16-day range sizes, for which environmental factors were included in the top model. This demonstrates that the areas where elephants are located (represented by the annual range area) are primarily structured by human presence and activity on the landscape, and it is only within those ranges that other environmental conditions start to influence elephant spatial patterns. The dominance of anthropogenic factors in affecting wildlife movement is increasingly common in species-level analyses.^{4,9,11,37–40}

Previous work suggests that there might be thresholds of human density above which elephants and humans cannot coexist.¹⁴ Our analysis identified HFI thresholds above which no collared elephants ranged (i.e., an HFI of 31.5 was the highest of any 16-day range value). These thresholds differed by location, which we attribute to differences in elephants' perception of risk to local human behavior. At different locations, human land-use and tolerance of elephants vary, as does the degree of enforcement of legal protection. A high human footprint in

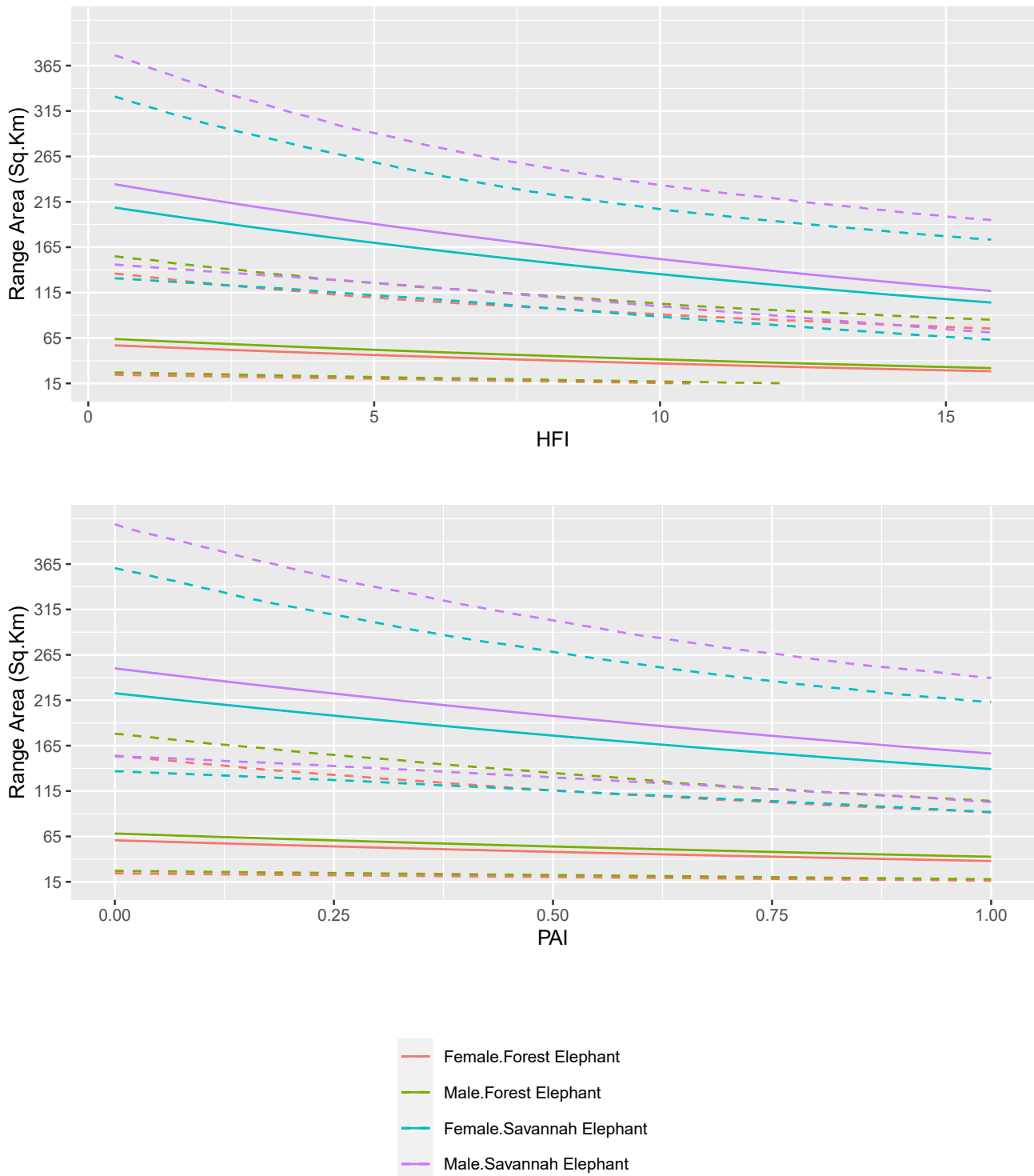


Figure 2. Annual elliptical time-density (ETD) 90th percentile range model

Variation in range sizes for both savannah and forest, and male and female elephants in relation to HFI) and PAI. Savannah elephants have larger ranges than forest elephants, and in both species, males have larger ranges than females. In both species, and for both sexes, range sizes decrease as HFI and PAI increase. We used the top selected annual range model (Table 1) to predict elephant range sizes (solid lines) across the support of a given continuous covariate (Table S5) while holding all other continuous covariates at their mean values. Model 95th percentile confidence intervals (dashed lines) were simulated by using random draws from the model parameter multivariate normal distribution.

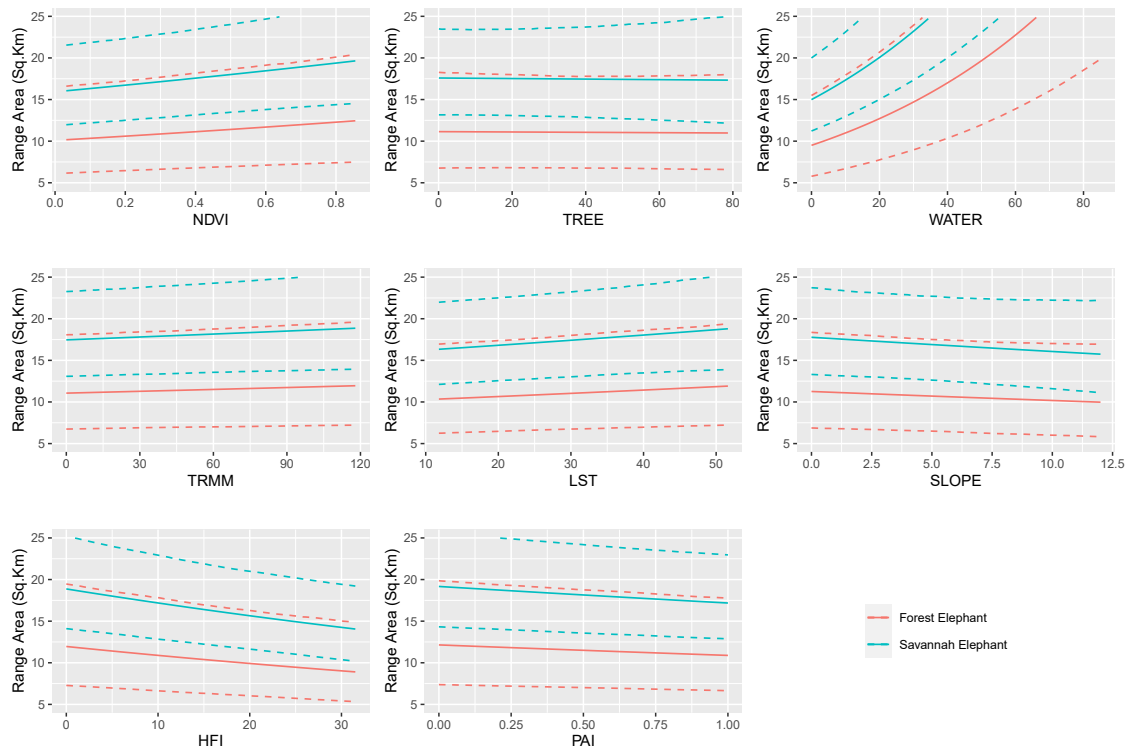


Figure 3. 16-Day elliptical time-density (ETD) 90th percentile range model

Variation in range sizes for both savannah and forest Elephants in relation to eight covariates. Range increases are associated with increases in NDVI,^{18,19} permanent water availability (WATER),²⁰ rainfall (TRMM),²¹ and LST.²² TREE^{23,24} has little effect on elephant range. Elephant range decreases are associated with increases in slope (SLOPE),²⁵ the HFI,^{15,26,27} and the PAI. We used the top selected model (Table 1) to predict elephant range sizes (solid lines) across the support of each successive continuous covariate (Table S5) while holding all other covariates at their mean values. Model 95th percentile confidence intervals (dashed lines) were simulated by using random draws from the model parameter multivariate normal distribution.

an elephant range also implies that people have easy access to elephant range, which might facilitate killing for ivory. This human predation itself might drive changes in elephant behavior; for example, both forest and savannah elephants become more nocturnal in response to poaching.^{41,42}

Our analysis demonstrated that range sizes were smaller for individuals whose ranges were contained more within protected areas, at both the annual and the 16-day time scales. Elephants often choose protected areas on account of the greater safety therein. In addition, protected areas might often supply undisturbed habitat and safe access to water.⁴³ Some protected areas also constrain elephant distribution by fences, such as the Kruger National Park and private conservancies both in South Africa and Kenya, though we lacked a data layer on fences to analyze this variable across Africa. Finally, protected areas can promote a high human footprint along their boundaries,^{44,45} which could also add to compression of elephant ranges within protected areas.

Within the annual range of the elephants studied, short-term 16-day range use was driven by a diversity of environmental covariates in addition to human factors. In contrast with theoretical models suggesting that movement, and ultimately space-use, should be lower where forage availability is higher,⁴⁶ elephants increased their movement and range sizes with increasing productivity over the shorter 16-day periods (although NDVI dropped

out of the top model for annual range). Similar relationships have been found in other, population-specific studies of elephants, which is thought to stem from dry season tethering to permanent water in arid and savannah systems.⁴⁷ Relatedly, water availability was positively associated with range size, suggesting where water was largely available, elephants ranged more broadly. These relationships were weaker in forest sites, where water is plentiful and not a limiting factor. Increased rainfall at the 16-day resolution was also associated with larger range sizes, though the effect was less than that of permanent water availability. Overall, this is consistent with results from other studies showing elephants range more broadly when water and food are more widely available in the rainy season.^{48–50} Interestingly, elephant range sizes also increased with temperature. We speculate that this might be related to evapotranspiration, given its correlation with temperature, which can amplify seasonal contrasts in water availability and productivity. Sixteen-day range size decreased with topographic slope, probably reflecting the avoidance of steep slopes because of the difficulty of moving across steep terrain and the energy required to do so.⁵¹

Geographical and historical conditions underpinning elephant range use

From the 16-day analysis, using the range of covariates under which the tracked elephants live, we derived a habitat suitability

model by using Google Earth Engine to measure the conditions in each kilometer square in Africa. It amounted to a potential elephant range of 18,169,219 km² covering 62% of the entire continent, excepting extreme habitats such as the Sahara, Kalahari, and Danakil deserts, urban areas, and high mountains. This represents areas likely occupied historically, highlighting that this generalist species can occupy the majority of ecosystems in Africa. By contrast, the African Elephant Specialist Group of IUCN's map of "known and possible ranges" today shows a range of 3,129,540 km² or 17.2% of the projected potential range that elephants probably once occupied. Of the habitat suitability model, 85% falls outside of protected areas whereas 57.4% of the Specialist Group's elephant range map falls outside of protected areas, suggesting elephants need areas larger than currently allocated for wildlife.

The existence of elephants in North Africa was well-known in classical times. The Phoenician navigator Hanno (500 BCE) saw elephants on the Atlantic coast of Africa. Herodotus (484–413 BCE) wrote of elephants in mountainous and thickly wooded land to the West of Lake Triton (in present day Tunisia). The record of extirpation of North African elephants was evident in the first century AD when Pliny the Elder wrote that "an ample supply of teeth (ivory) can now scarcely be found outside of India, the rest in our part of the world (North Africa) yielding to its appetite for luxury."¹ Previously, North African elephants were found from present day Agadir to Tunis. Our habitat suitability model indicates that almost exactly the same stretch of the Mediterranean littoral where elephants once existed is still suitable habitat today.

At the other end of the continent, Europeans first settled in the Cape in the 17th century where elephants abounded. In the next 250 years, hunting for ivory caused their near extinction from the southern tip of the continent to the Zambezi river.² Our model shows all of this stretch of Southern Africa, except for the Kalahari Desert, remains suitable habitat.

In West Africa, from the genetic analysis of ivory recovered from a Portuguese shipwreck in the 16th century, there is evidence of a reduction in genetic diversity compared with the genome of modern elephants,⁵² and this is attributed to the excessive killing of West African elephants. Likewise, in East Africa in the 19th century, large areas were emptied of elephants because of the ivory and slave trade.⁵³ Given the disparity between suitable elephant range and their actual range today, our data suggest that habitat incompatibility is unlikely to have been the cause of the elephant decline. It was most likely driven historically by human beings through excessive killing for ivory.

Our analysis demonstrates the fundamental role that humans currently play in shaping African elephant ranges at the continental scale. The human footprint is increasing at an accelerated rate and expected to double by 2050 (<https://population.un.org/wpp/Publications/>), with between 50%–70% of the planet already experiencing anthropogenic disturbance.^{10,54} Fragmentation of wildlife habitats by humans has resulted in only 7% of wildlife habitat patches being larger than 100 km.^{2,55} Clearly, if elephants are to persist in Africa, the spatial infrastructure driving socioeconomic development (e.g., roads and railways), must be strategically planned and

implemented.^{11,56} Development scenarios that accommodate the spatial needs of wildlife leaving large, low-human-impact areas of intact habitat, and especially formally protected areas, are urgently needed.⁵⁷ In the face of increasing human pressures, proactive landscape planning at the local, national, and continental scales are critical, as well as fostering an ethic of human-elephant coexistence if the future of elephants is to be secured. Is that too much to ask, in order to protect and conserve this signature animal even in a world where human well-being is paramount?

STAR METHODS

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2021.03.042>.

ACKNOWLEDGMENTS

The authors thank the European Commission (EC-MTKD-CT-2005-029893—SEARS, Spatial Economics and Remote Sensing of Elephant Resources) for funding a key meeting, and the Department of Zoology, Oxford University, for hosting it. The research was also supported financially by a Canadian National Science and Research Council (NSERC) PGSD3 (348450) award. The data were contributed by numerous colleagues researching elephant movements across Africa. We thank the range state governments, research authorities, and wildlife departments from Congo, Gabon, Central African Republic, Mali, Kenya, and South Africa. We also thank the African Elephant Conservation Fund of the United States Fish and Wildlife Service (USFWS); the United States Agency for International Development Central Africa Regional Program for the Environment (USAID CARPE); the Espèces Phares Project; the Central African Protected Areas Network of the European Union; Operation Loango; the Wildlife Conservation Society (WCS), Save the Elephants; the World Wide Fund For Nature-US; the Society for Conservation and Development; the Columbus Zoo; the Mara Elephant Project; the Safaricom Foundation; the Darwin Initiative; the WILD Foundation; Paul van Vliissingen; Caroline Tisdall; Susannah Rouse; the Sidekick Foundation; University of South Africa

(UNISA), and the Wildlife and Environmental Society of South Africa; the scientists who collaborated; and the guardians of national parks and national reserves across Africa.

AUTHOR CONTRIBUTIONS

J.W. helped conceive the study, ran analyses, wrote analysis code, helped collect tracking data in West and East Africa, and co-wrote manuscript. G.W. helped conceive the study, helped with analyses, helped collect tracking data in East Africa, and co-wrote manuscript. B.K. helped conceive the study, helped with analyses, and edited the manuscript. V.L. helped with statistical analyses and edited the manuscript. S.B. helped conceive the study, helped collect tracking data in Central Africa, and edited manuscript. S.S. helped conceive the study, helped with statistical analyses, and edited manuscript. M.H. helped conceive the study, helped with analyses, performed all fund-raising and data collection in Southern Africa, and edited manuscript. F.V. helped conceive the study, helped with funding, and co-wrote the manuscript. F.M. helped collect tracking data in Central Africa and edited manuscript. J.F. helped conceive the study, helped with funding, and helped with analyses. I.D.-H. helped conceive the study; helped with tracking data collection and funding in West, East, and South Africa; and co-wrote the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: December 29, 2020

Revised: February 5, 2021

Accepted: March 11, 2021

Published: April 1, 2021

REFERENCES

- Plinius Secundus Maior, C., Mayhoff, K.F.T., and Maior, C.P.S. (1906). *Naturalis Historiae* (Teubner).
- Bryden, H.A. (1903). The Decline and Fall of the South African Elephant. *Fortnightly Review* 73, 100–108.
- Douglas-Hamilton, I. (1987). African elephants: population trends and their causes. *Oryx* 27, 11–24.
- Maisels, F., Strindberg, S., Blake, S., Wittemyer, G., Hart, J., Williamson, E.A., Aba'a, R., Abitsi, G., Ambahe, R.D., Amsini, F., et al. (2013). Devastating decline of forest elephants in central Africa. *PLoS ONE* 8, e59469.
- Thouless, C.R., Dublin, H.T., Blanc, J.J., Skinner, D.P., Daniel, T.E., Taylor, R.D., Maisels, F., Frederick, H.L., and Bouché, P. (2016). African Elephant Status Report 2016: An update from the African Elephant Database (Occasional Paper Series of IUCN Species Survival Commission, No. 60 IUCN/SSC African Elephant Specialist Group).
- Robson, A.S., Trimble, M.J., Purdon, A., Young-Overton, K.D., Pimm, S.L., and van Aarde, R.J. (2017). Savanna elephant numbers are only a quarter of their expected values. *PLoS ONE* 12, e0175942.
- Wittemyer, G., Northrup, J.M., Blanc, J., Douglas-Hamilton, I., Omondi, P., and Burnham, K.P. (2014). Illegal killing for ivory drives global decline in African elephants. *Proc. Natl. Acad. Sci. USA* 111, 13117–13121.
- Wall, J., Wittemyer, G., LeMay, V., Douglas-Hamilton, I., and Klinkenberg, B. (2014). Elliptical Time-Density model to estimate wildlife utilization distributions. *Methods Ecol. Evol.* 5, 780–790.
- Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C., Ali, A.H., Allen, A.M., Attias, N., Avgar, T., et al. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science* 359, 466–469.
- Barnosky, A.D., Hadly, E.A., Bascompte, J., Berlow, E.L., Brown, J.H., Fortelius, M., Getz, W.M., Harte, J., Hastings, A., Marquet, P.A., et al. (2012). Approaching a state shift in Earth's biosphere. *Science* 324, 52–58.
- Blake, S., Deem, S.L., Strindberg, S., Maisels, F., Momont, L., Isia, I.-B., Douglas-Hamilton, I., Karesh, W.B., and Kock, M.D. (2008). Roadless wilderness area determines forest elephant movements in the Congo Basin. *PLoS ONE* 3, e3546.
- Douglas-Hamilton, I., Krink, T., and Vollrath, F. (2005). Movements and corridors of African elephants in relation to protected areas. *Naturwissenschaften* 92, 158–163.
- Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V., and Douglas-Hamilton, I. (2013). Characterizing properties and drivers of long distance movements by elephants (*Loxodonta africana*) in the Gourma, Mali. *Biol. Conserv.* 157, 60–68.
- Hoare, R.E., and Du Toit, J.T. (1999). Coexistence between people and elephants in African savannas. *Conserv. Biol.* 13, 633–639.
- IUCN and UNEP-WCMC (2013). The World Database on Protected Areas (WDPA) (www.protectedplanet.net, Accessed: Aug 30, 2013) (Protected Planet).
- Burnham, K.P., and Anderson, D.R. (2002). *Model Selection and MultiModel Inference: A Practical Information-Theoretic Approach, Second Edition* (Springer-Verlag New York, Inc.).
- Akaike, H. (1974). A New Look at the Statistical Model Identification. *IEEE Trans. Automat. Contr.* 19, 716–723.
- Huete, A., Didan, K., Miura, T., Rodriguez, E.P., Gao, X., and Ferreira, L.G. (2002). Overview of the radiometric and biophysical performance of the MODros. *Inf. Serv. vegetation indices. Remote Sens. Environ.* 83, 195–213.
- NASA LP DAAC (2017). MODros. *Inf. Serv. MCD43A4 (NDVI): MODros. Inf. Serv./Terra and Aqua Nadir BRDF-Adjusted Reflectance Daily L3 Global 500 m SIN Grid. Version 5 (NASA EOSDros. Inf. Serv. Land Processes DAAC, USGS Earth Resources Observation and Science (EROS) Center)*. <https://lpdaac.usgs.gov>.
- Pekel, J.-F., Cottam, A., Gorelick, N., and Belward, A.S. (2016). High-resolution mapping of global surface water and its long-term changes. *Nature* 540, 418–422.
- NASA GSFC (2017). Tropical Rainfall Monitoring Mission (TRMM) 2F3B42 3-Hour 0.25-degree product. Version 7. (NASA Goddard Space Flight Centre. <https://trmm.gsfc.nasa.gov/>).
- NASA LP DAAC (2017). MODros. *Inf. Serv./Terra MOD11A2 Land Surface Temperature/Emissivity 8-Day L3 Global 1 km SIN Grid. Version 5 (NASA EOSDros. Inf. Serv. Land Processes DAAC, USGS Earth Resources Observation and Science (EROS) Center)*. <https://lpdaac.usgs.gov>.
- Carroll, M., Townshend, J., Hansen, M., DiMiceli, C., Sohlberg, R., and Wurster, K. (2011). MODros. *Inf. Serv. Vegetative Cover Conversion and Vegetation Continuous Fields. In Land Remote Sensing and Global Environmental Change: NASA's Earth Observing System and the Science of ASTER and MODros. Inf. Serv. B. Ramachandran, C.O. Justice, and M.J. Abrams, eds. (Springer-Verlag), p. 873.*
- NASA LP DAAC (2017). MODros. *Inf. Serv. MOD44B: MODros. Inf. Serv./Terra Vegetation Continuous Fields Yearly L3 Global 250 m SIN Grid. Version 5.1 (NASA EOSDros. Inf. Serv. Land Processes DAAC, USGS Earth Resources Observation and Science (EROS) Center)*. <https://lpdaac.usgs.gov>.
- Kobrick, M., and Crippen, R. (2013). NASA Shuttle Radar Topography Mission 1 arcsecond Global Digital Elevation Model (HDF-EOS).
- Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., and Woolmer, G. (2002). The Human Footprint and the Last of the Wild. *Bioscience* 52, 891.
- Venter, O., Sanderson, E.W., Magrath, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., et al. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat. Commun.* 7, 12558.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., et al.

- (2013). High-resolution global maps of 21st-century forest cover change. *Science* 342, 850–853.
29. Wall, J. (2014). ArcMET: Movement Ecology Tools for ArcGIS. In *Symposium on Animal Movement and the Environment*.
 30. Rasmussen, H.B. (2005). PhD Thesis: Reproductive tactics in male African savannah elephants (*Loxodonta africana*) (Oxford University).
 31. Taylor, L.A., Vollrath, F., Lambert, B., Lunn, D., Douglas-Hamilton, I., and Wittemyer, G. (2020). Movement reveals reproductive tactics in male elephants. *J. Anim. Ecol.* 89, 57–67.
 32. Shannon, G., Page, B.R., Duffy, K.J., and Slotow, R. (2006). The role of foraging behaviour in the sexual segregation of the African elephant. *Oecologia* 150, 344–354.
 33. Lindsay, K. (2011). Habitat Use, Diet Choice, and Nutritional Status in Female and Male Amboseli Elephants. In *The Amboseli Elephants: A Long-term perspective on a long-lived mammal*, C.J. Moss, H. Croze, and P. Lee, eds. (The University of Chicago Press), pp. 51–73.
 34. Bastille-Rousseau, G., and Wittemyer, G. (2019). Leveraging multidimensional heterogeneity in resource selection to define movement tactics of animals. *Ecol. Lett.* 22, 1417–1427.
 35. Campos-Arceiz, A., and Blake, S. (2011). Megagardeners of the forest - the role of elephants in seed dispersal. *Acta Oecol.* 37, 542–553.
 36. Schuttler, S.G., Blake, S., and Eggert, L.S. (2012). Movement Patterns and Spatial Relationships Among African Forest Elephants. *Biotropica* 44, 445–448.
 37. Barnes, R.F.W., Barnes, K.L., Alers, M.P.T., and Blom, A. (1991). Man determines the distribution of elephants in the rain forests of northern Gabon. *Afr. J. Ecol.* 29, 54–63.
 38. Bastille-Rousseau, G., Wall, J., Douglas-Hamilton, I., Lesowapir, B., Loloju, B., Mwangi, N., and Wittemyer, G. (2019). Landscape-scale habitat response of African elephants shows strong selection for foraging opportunities in a human dominated ecosystem. *Ecography* 43, 149–160.
 39. de Boer, W.F., van Langevelde, F., Prins, H.H.T., de Ruiter, P.C., Blanc, J., Vis, M.J.P., Gaston, K.J., and Douglas-Hamilton, I. (2013). Understanding spatial differences in African elephant densities and occurrence, a continent-wide analysis. *Biol. Conserv.* 159, 468–476.
 40. Roever, C.L., van Aarde, R.J., and Chase, M.J. (2013). Incorporating mortality into habitat selection to identify secure and risky habitats for savannah elephants. *Biol. Conserv.* 164, 98–106.
 41. Breuer, T., Maisels, F., and Fishlock, V. (2016). The consequences of poaching and anthropogenic change for forest elephants. *Conserv. Biol.* 30, 1019–1026.
 42. Ihwagi, F.W., Thouless, C., Wang, T., Skidmore, A.K., Omondi, P., and Douglas-Hamilton, I. (2018). Night-day speed ratio of elephants as indicator of poaching levels. *Ecol. Indic.* 84, 38–44.
 43. Loarie, S.R., Aarde, R.J.V., and Pimm, S.L. (2009). Fences and artificial water affect African savannah elephant movement patterns. *Biol. Conserv.* 142, 3086–3098.
 44. Douglas-Hamilton, I. (1972). On the ecology and behaviour of the African elephant. <https://www.worldcat.org/title/on-the-ecology-and-behaviour-of-the-african-elfphant-the-elfphants-of-lake-manyara/oclc/17554601>.
 45. Wittemyer, G., Elsen, P., Bean, W.T., Burton, A.C.O., and Brashares, J.S. (2008). Accelerated human population growth at protected area edges. *Science* 321, 123–126.
 46. Charnov, E.L. (1976). Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9, 129–136.
 47. Redfern, J.V., Grant, R., Biggs, H., and Getz, W.M. (2003). Surface-Water Constraints on Herbivore Foraging in the Kruger National Park, South Africa. *Ecology* 84, 2092–2107.
 48. Wittemyer, G., Getz, W.M., Vollrath, F., and Douglas-Hamilton, I. (2007). Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. *Behav. Ecol. Sociobiol.* 61, 1919–1931.
 49. Western, D., and Lindsay, W.K. (1984). Seasonal herd dynamics of a savanna elephant population. *Afr. J. Ecol.* 22, 229–244.
 50. Young, K.D., Ferreira, S.M., and Van Aarde, R.J. (2009). Elephant spatial use in wet and dry savannas of southern Africa. *J. Zool.* 278, 189–205.
 51. Wall, J., Douglas-Hamilton, I., and Vollrath, F. (2006). Elephants avoid costly mountaineering. *Curr. Biol.* 16, R527–R529.
 52. de Flamingh, A., Coutu, A., Sealy, J., Chirikure, S., Bastos, A.D.S., Libanda-Mubusisi, N.M., Malhi, R.S., and Roca, A.L. (2020). Sourcing Elephant Ivory from a Sixteenth-Century Portuguese Shipwreck. *Curr. Biol.* 621–628.
 53. Alpers, E.A. (1975). Ivory and Slaves: Changing Pattern of International Trade in East Central Africa to the Later Nineteenth Century (University of California Press).
 54. Bar-On, Y.M., Phillips, R., and Milo, R. (2018). The biomass distribution on Earth. *Proc. Natl. Acad. Sci. USA* 115, 6506–6511.
 55. Ibisch, P.L., Hoffmann, M.T., Kreft, S., Pe'er, G., Kati, V., Biber-Freudenberger, L., DellaSala, D.A., Vale, M.M., Hobson, P.R., and Selva, N. (2016). A global map of roadless areas and their conservation status. *Science* 354, 1423–1427.
 56. Laurance, W.F., Clements, G.R., Sloan, S., O'Connell, C.S., Mueller, N.D., Goosem, M., Venter, O., Edwards, D.P., Phalan, B., Balmford, A., et al. (2014). A global strategy for road building. *Nature* 513, 229–232.
 57. Laurance, W.F., and Arrea, I.B. (2017). Roads to riches or ruin? *Science* 358, 442–444.
 58. Lee, P.C., Sayialel, S., Lindsay, W.K., and Moss, C.J. (2012). African elephant age determination from teeth: Validation from known individuals. *Afr. J. Ecol.* 50, 9–20.
 59. Worton, B.J. (1989). Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. *Ecology* 70, 164–168.
 60. Mohr, C.O. (1947). Table of equivalent populations of North American small mammals. *Am. Midl. Nat.* 37, 223–249.
 61. Gao, B.C. (1996). NDWI - A normalized difference water index for remote sensing of vegetation liquid water from space. *Remote Sens. Environ.* 58, 257–266.
 62. NASA LP DAAC (2017). MODros. Inf. Serv. MCD43A4 (NDWI): MODros. Inf. Serv./Terra and Aqua Nadir BRDF-Adjusted Reflectance Daily L3 Global 500 m SIN Grid. Version 5 (NASA EOSDros. Inf. Serv. Land Processes DAAC, USGS Earth Resources Observation and Science (EROS) Center). <https://lpdaac.usgs.gov>.
 63. NASA LP DAAC (2017). MODros. Inf. Serv. MCD43A4 (EVI): MODros. Inf. Serv./Terra and Aqua Nadir BRDF-Adjusted Reflectance Daily L3 Global 500 m SIN Grid. Version 5 (NASA EOSDros. Inf. Serv. Land Processes DAAC, USGS Earth Resources Observation and Science (EROS) Center). <https://lpdaac.usgs.gov>.
 64. Carter, N., Williamson, M., Gilbert, S., Lischka, S., Prugh, L., Lawler, J., Metcalf, A., Jacob, A., Beltrán, B., Castro, A.J., et al. (2019). Integrated spatial analysis for human-wildlife coexistence in the American West. *Environ. Res. Lett.* 15, 021001..
 65. de Beer, Y., and van Aarde, R.J. (2008). Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas? *J. Arid Environ.* 72, 2017–2025.
 66. Grainger, M., Aarde, R., and Whyte, I. (2005). Landscape heterogeneity and the use of space by elephants in the Kruger National Park, South Africa. *Afr. J. Ecol.* 43, 369–375.
 67. Gelman, A., and Hill, J.C. (2007). *Data analysis using regression and multi-level/hierarchical models* (Cambridge University Press).
 68. Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R*. M. Gail, K.

- Krickeberg, J.M. Samet, A. Tsiatis, and W. Wong, eds. (Springer New York).
69. Pinheiro, J.C., and Bates, D. (2000). *Mixed effects models in S and S-Plus* (Springer Verlag).
 70. Pinheiro, J.C., and Bates, D. (2013). R Documentation (Package: nlme - Linear Mixed-Effects Models) lme function (URL: <http://stat.ethz.ch/R-manual/R-patched/library/nlme/html/lme.html>, Accessed: Nov 4, 2014).
 71. Schabenberger, O., and Pierce, F.J. (2001). *Contemporary statistical models for the plant and soil sciences* (CRC Press).
 72. West, B., Welch, K.B., and Galecki, A.T. (2007). *Linear Mixed Models: A Practical Guide Using Statistical Software, First Edition* (Chapman & Hall/CRC).
 73. R Core Team R. (2018). R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing. URL: <http://www.r-project.org>).

STAR★METHODS

KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---|--------------------------|---|
| Software and Algorithms | | |
| ArcMET: Movement Ecology Tools for ArcGIS | Wall et al. ⁸ | www.movementecology.net |
| analysis_worksheet.ipynb | This Paper | https://github.com/walljcg/panafel |

RESOURCE AVAILABILITY

Lead contact

Further information and requests for information and data related to this analysis should be directed to the lead contact: Jake Wall (jake@maraelephantproject.org or walljcg@gmail.com).

Materials availability

This study did not generate any materials.

Data and code availability

Given the sensitive nature of the location of elephants due to the ongoing illegal killing of elephants for ivory, tracking data will be made available upon written request to the lead author rather than made public. Analysis code used in this study is available at: <https://github.com/walljcg/panafel>.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Ethics statement

All elephant captures were carried out according to the practice and authorisation of the veterinary services of the relevant range states.

Extended acknowledgments

We thank the Google Earth Engine and Outreach teams for their support and funding in this work, in particular, Rebecca Moore, Tanya Birch, Sean Askay, David Thau and Tyler Erickson. We also thank the Esri Conservation Programme especially David Gadsden, Charles Convis, Steve Beckwitt and Esri East Africa who made Esri software available for our research.

Forest

Funding and logistical assistance

The African Elephant Conservation Fund of the United States Fish and Wildlife Service (USFWS); United States Agency for International Development Central Africa Regional Program for the Environment (US-AID CARPE); the Espesces Phares Project and the Central African Protected Areas Network of the European Union; Operation Loango; Wildlife Conservation Society (WCS), Save the Elephants; World Wide Fund For Nature WWF-US; the Society for Conservation and Development, and the Columbus Zoo.

Permissions and collaboration

The research authorities and wildlife departments from Congo, Gabon, and Central African Republic; Veterinarians who put collars on: Billy Karesh, Sharon L. Deem and Mike Kock. Congo/CR/Gabon tracking team members: Gregoire Mambelele, Eric Mossimbo, Lamba Michel, Zomimputu, Loya, Sylvan Imalimo and Mammadou Gassagna; Data collectors (Gabon): Ludovic Momont, Nerissa Chao, Julian Eastwood, Erica Spotswood; Logistics: Mike Fay, Bryan Curran, Djoni-Djimbi Bourges, Paul and Sarah Elkan, Kate Abernethy, Nigel Orbell, Lee White, Tommy Smith, Lisa Steel, Allard Blom, Pauwel deWachter, Mark Ella Akou, and Patrick Koumbi.

Savannah

We thank the Kenyan Office of the President of the Republic of Kenya, the Samburu, Isiolo and Narok County governments, the Kenya Wildlife Service for collaboration including veterinary services, and Save the Elephants and Mara Elephant Project for data and field operations. We thank the following individuals: from KWS Patrick Omondi, Matthew Mutinda, Francis Gakuya, Geoffrey Chege, from Save the Elephants, Frank Pope, Ben Okita, Lucy King, Festus Ihwagi, David Daballen, Chris Leadismo, Benjamin Loloju, Nelson Mwangi, Gilbert Sabinga, David Kimanzi, Jerenimo Lepirei, Wilson Lelukumani, and Barnerd Lesowapir. From the Mara Elephant

Project we thank Marc Goss, Wilson Sairowua, Zakayo Naeku, Jackson Maitai, Madeleine Goss, Richard Roberts, and the Fehsenfeld family for contribution of both data and funding. We also thank Dr. Henrik Rasmussen from Savannah Tracking Ltd.

Sahel

Data Collection

Save the Elephants; Funding: Save the Elephants & the WILD Foundation; We also thank the Wildlife Conservation Society, El Media Doumbia, Vance Martin, Susan Canney, Mike Deutsch, the Save the Elephants collaring team in 2008, the Government of Mali and African Parks Foundation.

METHOD DETAILS

GPS collar data

Tracking data were collected from elephants inhabiting 19 distinct geographic sites from six elephant range states (Figure 1, Table S1, Data S1). The sites studied cover four African biomes: Savannah (East Africa), Forest (Central Africa), Sahel (West Africa), and Bushveld (South Africa). Individual elephants were fitted with GPS radio collars (Tables S1 and S2).

GPS collar deployment was focused on elephants inhabiting IUCN category I and II protected areas in each site, generally thought to represent better protected populations. Immobilization and collar fitting followed national procedures established by the national veterinary services in each country. During capture, the gender of each elephant was recorded, and ages were estimated where possible based on body size and molar progression⁵⁸ although ages were not used in the analysis. Collated datasets we believe represented the full range of each explanatory variable (Tables S5).

18 different types of GPS radio collars were used. Collars transmitted data remotely through satellite or local mobile phone networks or were manually downloaded and processed. Different duty cycles were used because of limitations of collar battery life relative to data collection objectives in the different study systems and ranged from 15 to 2,400-min intervals, with most animal locations sampled every 60-min (Table S2).

In total, 254 individual adult elephants were tracked: 120 females and 134 males; 220 savannah and 34 forest elephants, resulting in 3,219,375 positions recorded between 1998 and 2013. Collar datasets had a median of 7,417 positions and Interquartile Range (IQR) of between 2,245 and 19,173 positions per individual. Average tracking duration was 590 days per individual, with 171 (68%) individuals having greater than one year of data and 109 having multi-year datasets. Prior to analysis, these data were filtered keeping only those datasets with a minimum of 12 h sampling (i.e., no separation in successive data points greater than 12 h) resulting in 2,947,767 analyzed locations representing 108 females and 121 males included in analyses (Table S1, Data S1).

Study sites

The six sites in Central Africa were in predominantly high canopy tropical forest with on average > 1,400 mm of rainfall annually. West Africa was represented by one site the Gourma in Mali—ranging from Sahelian (110 mm annual rainfall) to Sudano-savannah vegetation (600 mm annual rainfall). East African savannah systems with annual rainfall varying between 200 to 800 mm per year were represented by nine sites. South African bushveld, with annual rainfall averaging 600 mm, was represented by three sites.

Elliptical time-density ranges

We calculated range areas at two temporal scales: sequential 16-day periods and sequential annual periods, resulting in 10,319 (16-day) and 302 (annual) Elliptical Time-Density (ETD) range areas. The ETD method accounts for the time between fixes and the overall speed-distribution of the animal to generate an estimated spatial utilization distribution,⁸ from which we calculated the area where the animal spent 90% of its time during the tracking period. This range estimator adheres closely to the observed locations (occurrence estimation), where smoothing around the observed locations represents plausible areas of occurrence within the time interval of observed locations. We used this method to ensure our regression analysis of covariates in an elephant's range represented the area the animal likely occurred rather than potentially could have used (as represented by other range methods with more liberal smoothing algorithms such as Bivariate Gaussian Kernel Density estimation). Second, this method adjusts interpolation between fixes based on the sampling resolution and biologically derived movement parameters, ensuring comparable representation across tracking records with different sampling regimes and error rates. Speed distributions for each animal were parameterized using a two-parameter Weibull distribution fit using maximum likelihood methods. The 90th percentile speed-distribution value was used as the upper speed cut-off.⁸

For comparison of the ETD areal estimates with traditional methods (more commonly found in the published literature) we also calculated 90th percentile Kernel Density Estimate (KDE)⁵⁹ and Minimum Convex Polygon (MCP)⁶⁰ range areas (Table S3). Comparison of ETD with other utilization distribution estimators found the ETD method had lower overall error in representing space-use at the 90th percentile range area.⁸

Covariates

For each ETD range polygon and its associated time span, we extracted a series of covariate information derived from satellite imagery and other spatial datasets (Table S4). Raster calculations were made using the Google Earth Engine (GEE) remote sensing platform²⁸ at a resolution of 0.25 km². We averaged across time and space the values of raster pixels to obtain a single mean value for

each covariate for each ETD range for each time span. Specifically, we extracted information on vegetative properties of the landscape using the Moderate-resolution Imaging Spectro-radiometer (MODIS) Normalized Difference Vegetation Index (NDVI),^{18,19} Normalized Difference Water Index (NDWI),^{61,62} Enhanced Vegetation Index (EVI),^{18,63} and percent tree cover (TREE).^{23,24} Abiotic features, namely slope derived from NASA's Shuttle Radar Topography Mission (SLOPE),²⁵ land surface temperature (LST),²² rainfall (TRMM),²¹ and permanent water availability (WATER)²⁰ were also extracted in GEE. Finally, we extracted information on the overlap between range and protected area boundaries (PAI) (as defined by the World Database on Protected Areas (WDPA)¹⁵) and the Human Footprint Index (HFI),^{26,27} an index of the aggregate influence of human population density, built-up areas, night-time lights, land use, coastlines, roads, railroads, and navigable rivers. See Table S4 for further details on model covariates.

Data were categorized according to species (Savannah elephants *L. africana* or Forest elephants *L. cyclotis*), sex (Male or Female), the site where an animal was collared (Table S1), and the individual animal identifier.

Given the scale of this analysis, we relied on coupling movement data with relatively high resolution, standardized global datasets facilitated by the Google Earth Engine analytical environment.²⁸ While these data offer powerful, standardized information enabling such a broad, continental scale analysis, we were still missing some finer resolution layers on different anthropogenic and environmental variables that could not be compiled systematically across the diversity of ecosystems in this study. In particular, we were not able to assemble comprehensive spatial metrics of risk to elephants. As discussed in relation to variable range sizes found in areas of high human impact, understanding the tolerance of local people to elephants is critical to understanding ranging behavior, but such spatially explicit information on human perception is rare.⁶⁴ While several systems in this study have fenced boundaries, a factor known to restrict normative elephant movement behavior and space use, we lacked systematic information on fences across all studied populations. We also lacked high quality layers on the vegetation community, including tree fruiting phenology, relying on a coarse tree cover layer, which we found had a positive impact on range size. The spatial configuration of the vegetation community is widely recognized as influential on range geometry and size.^{65,66} While we incorporated permanent water in our analysis, seasonal or ephemeral water sources are more difficult to characterize, limiting inference on some of the more dynamic aspects of this important abiotic correlate of movement.

Given the dominant influence of land use change on habitat and species loss, the projected human population growth and land use plans in Africa will be the critical challenge for wildlife conservation in the future. Increasing the resolution, availability, and accuracy of global landscape layers will facilitate assessment of the impacts of human population expansion on wildlife, as well as identifying approaches to mediate such impacts by identifying those areas with the greatest long-term conservation viability.

QUANTIFICATION AND STATISTICAL ANALYSIS

We developed sets of linear mixed-effects models, with individual id as a random effect, at both the 16-day and annual timescales relating the effects of covariates to range area to answer Question 1 (How do elephant home ranges vary in size across sexes, species, and biome?), and Question 2 (How influential are individual, biotic, abiotic and anthropogenic factors on elephant range size?). Models were classified according to: i) *indv* – models containing individual factors of sex or species, ii) *anthro* – models containing anthropogenic factors of protected area use and the human footprint, iii) *biotic* – models containing variables related to the biotic environment including vegetation indices and tree cover, iv) *abiotic* – models containing variables related to the abiotic environment including slope, temperature, rainfall and water, v) *full* – models containing all model variables, or; vi) *mixed* - models that contained variables from a combination of driver categories.

Model specification

Range areas were log-transformed to account for their exponential distribution and non-negative values.^{67,68} We used a nested *var-Ident* variance structure^{69,70} to allow for heterogeneous spread in the residuals associated with individuals nested within sites. The random-effects structure of the models (individuals nested within sites) and the heterogeneous variance structure (variance allowed to vary per site) helped to account for the sampling biases across sites. All continuous covariates were standardized $\frac{X - \mu_x}{\sigma_x}$ and tested for pairwise correlations (Figure S1, Figure S2) before model fitting. Because of a high degree of correlation (> 0.7) between NDVI, EVI, and NDWI at the 16-day scale, we first tested three models with each of these covariates individually, based on the Corrected Akaike's Information Criterion (AICc),^{16,17} and dropped EVI and NDWI from further analysis (Figure S1). At annual scales, there was a high degree of correlation (> 0.7) between NDVI, EVI, LST, and TREE covariates. Model selection favored NDVI for the full model specification (Figure S2). All other covariates had less than 0.7 pairwise correlation and were included in the same models.

The full model specification for the 16-day model, in terms of a single observation of range area for animal *i* nested within site *j* at time *t*, was:

$$\log(\text{AREA}_{ijt}) \sim \gamma_j + \alpha_{ij} + \text{SEX}_{ijt} + \text{SPECIES}_{ijt} + \text{NDVI}_{ijt} + \text{TREE}_{ijt} + \text{LST}_{ijt} + \text{TRMM}_{ijt} + \text{WATER}_{ijt} + \text{SLOPE}_{ijt} + \text{HFI}_{ijt} + \text{PAI}_{ijt} + \epsilon_{ijt}$$

while the full model specification for the annual model was:

$$\log(\text{AREA}_{ijt}) \sim \gamma_j + \alpha_{ij} + \text{SEX}_{ijt} + \text{SPECIES}_{ijt} + \text{NDVI}_{ijt} + \text{NDWI}_{ijt} + \text{TRMM}_{ijt} + \text{WATER}_{ijt} + \text{SLOPE}_{ijt} + \text{HFI}_{ijt} + \text{PAI}_{ijt} + \epsilon_{ijt}$$

where a random intercept α_{ij} is specified for each individual, and a random intercept γ_j is specified for each local site, the within-animal residuals are given by ε_{ijt} . The parameters α_{ij} , γ_j and ε_{ijt} were assumed to follow normal distributions.

An exponential decay in covariance between sequential observations of each individual animal was modeled with an absolute difference in time (i.e., autocorrelation structure of order 1 with a continuous time covariate that allows for the exponential decay of correlation with temporal distance (CorCAR1)).⁷¹ The residual covariance matrix was modeled as a block diagonal with zeros on non-diagonal entries indicating independence of inter-animal within site errors.

Random effects were used in both the annual and 16-day models to account for individual random variability nested within site-based random variability, and both were highly significant (Table S6). The total explained variance (conditional) of the 16-day model was 44.80% and 81.3% for the annual model (Table S6). The temporal correlation CorCAR1 parameter f (calculated based on years from the start of a dataset) was also significant in both the 16-day ($f = 1.71E-6$) and annual models ($f = 0.35$) indicating temporal autocorrelation was significant and needed to be accounted for in our modeling approach (Table S6).

Model selection

The Corrected Akaike's Information Criterion (AICc)^{16,17} was used to select between our competing movement hypotheses (models) at both the 16-day and annual time frames. Final models were re-fit using restricted maximum likelihood (REML) to provide reliable estimates for regression parameters.⁷² Model fit was also assessed using graphical methods.⁶⁸ Statistical modeling was performed using R software.⁷³

Habitat suitability model

To answer Question 3, (how much suitable elephant habitat remains across Africa and how much of this suitable habitat is currently occupied?), we calculated a habitat suitability model (HSM) to be any geographical location with conditions that fell within the range of mean values encountered by an elephants' 16-day ETD range (i.e., every 1.0 km² location within the African continent was assessed by whether or not the values of the covariates NDVI, SLOPE, LST etc. intersected the range of conditions recorded by any elephant's 16-day ETD range within our study). The HSM was generated using Google Earth Engine. Further details and code for our modeling procedure can be found in the analysis_worksheet.ipynb jupyter notebook available at: <https://github.com/walljcg/panafel>.