

Current Biology

Environmental and anthropogenic factors synergistically affect space use of jaguars

Highlights

- Jaguar space use and movements relate consistently to landscape factors
- Forest cover, net primary productivity, and road density are key factors
- Jaguars perceive their environment equally, irrespective of location or ecoregion
- Our results have applications to jaguar conservation throughout the species' range

Authors

Jeffrey J. Thompson,
Ronaldo G. Morato,
Bernardo B. Niebuhr, ...,
Yamil E. Di Blanco,
Alexandre M.C. Lopes,
Milton Cezar Ribeiro

Correspondence

jthompson.py@gmail.com

In brief

Thompson et al. analyze 115 telemetry datasets from jaguars to show spatial needs and movements are predictably related to environmental and human factors across the species' range. The range-wide consistency in jaguar space use and movements to landscape factors has applications to the conservation of the species throughout its distribution.

Report

Environmental and anthropogenic factors synergistically affect space use of jaguars

Jeffrey J. Thompson,^{1,2,46,47,*} Ronaldo G. Morato,³ Bernardo B. Niebuhr,^{3,4,5,6} Vanesa Bejarano Alegre,⁴ Júlia Emi F. Oshima,⁴ Alan E. de Barros,⁷ Agustín Paviolo,^{8,9} J. Antonio de la Torre,^{10,11} Fernando Lima,^{4,12} Roy T. McBride, Jr.,¹³ Rogerio Cunha de Paula,³ Laury Cullen, Jr.,¹² Leandro Silveira,¹⁴ Daniel L.Z. Kantek,¹⁵ Emiliano E. Ramalho,^{5,16} Louise Maranhão,¹⁶ Mario Haberfeld,^{17,18,19} Denis A. Sana,^{5,20} Rodrigo A. Medellin,²¹ Eduardo Carrillo,²² Victor H. Montalvo,^{22,23} Octavio Monroy-Vilchis,²⁴ Paula Cruz,^{8,9} Anah T.A. Jacomo,¹⁴ Giselle B. Alves,^{14,25} Ivonne Cassaigne,²⁶ Ron Thompson,²⁶ Carolina Sáenz-Bolaños,^{22,23} Juan Carlos Cruz,^{23,27}

(Author list continued on next page)

¹Asociación Guyra Paraguay and CONACYT, Parque Ecológico Asunción Verde, Asunción, Paraguay

²Instituto Saite, Asunción, Paraguay

³Centro Nacional de Pesquisa e Conservação de Mamíferos Carnívoros, Instituto Chico Mendes de Conservação da Biodiversidade, Atibaia, SP 12952011, Brazil

⁴Instituto de Biociências, Universidade Estadual Paulista-UNESP, Departamento de Biodiversidade, Laboratório de Ecologia Espacial e Conservação LEEC, Rio Claro, SP 13506900, Brazil

⁵Instituto Pró-Carnívoros, Atibaia, SP 12945010, Brazil

⁶Department of Animal Nutrition and Management, Swedish University of Agricultural Sciences, Uppsala, Sweden

⁷Instituto de Biociências, Departamento de Ecologia, Universidade de São Paulo, Rua do Matão, Trav. 14, no. 321, Cidade Universitária, São Paulo, SP 05508-090, Brazil

⁸Instituto de Biología Subtropical, Universidad Nacional de Misiones and CONICET, Puerto Iguazú, Misiones 3370, Argentina

⁹Asociación Civil Centro de Investigaciones del Bosque Atlántico, Puerto Iguazú, Misiones 3370, Argentina

¹⁰Programa Jaguar de la Selva Maya, Bioconciencia A.C., Ciudad de México, México

¹¹School of Environmental and Geographical Sciences, University of Nottingham Malaysia, Jalan Broga, 43500 Semenyih, Selangor, Malaysia

¹²IPÊ-Instituto de Pesquisas Ecológicas, Nazaré Paulista, SP 12960000, Brazil

¹³Faro Moro Eco Research, Estancia Faro Moro, Departamento de Boquerón, Paraguay

(Affiliations continued on next page)

SUMMARY

Large terrestrial carnivores have undergone some of the largest population declines and range reductions of any species, which is of concern as they can have large effects on ecosystem dynamics and function.^{1–4} The jaguar (*Panthera onca*) is the apex predator throughout the majority of the Neotropics; however, its distribution has been reduced by >50% and it survives in increasingly isolated populations.⁵ Consequently, the range-wide management of the jaguar depends upon maintaining core populations connected through multi-national, transboundary cooperation, which requires understanding the movement ecology and space use of jaguars throughout their range.^{6–8} Using GPS telemetry data for 111 jaguars from 13 ecoregions within the four biomes that constitute the majority of jaguar habitat, we examined the landscape-level environmental and anthropogenic factors related to jaguar home range size and movement parameters. Home range size decreased with increasing net productivity and forest cover and increased with increasing road density. Speed decreased with increasing forest cover with no sexual differences, while males had more directional movements, but tortuosity in movements was not related to any landscape factors. We demonstrated a synergistic relationship between landscape-scale environmental and anthropogenic factors and jaguars' spatial needs, which has applications to the conservation strategy for the species throughout the Neotropics. Using large-scale collaboration, we overcame limitations from small sample sizes typical in large carnivore research to provide a mechanism to evaluate habitat quality for jaguars and an inferential modeling framework adaptable to the conservation of other large terrestrial carnivores.

RESULTS

The distribution of the jaguar has been greatly reduced due to habitat loss and persecution so that it now occupies about 50% of its original range,^{5,9} and not surprisingly, the distribution of the jaguar is highly associated with habitat availability and low

levels of anthropogenic impacts.¹⁰ Although jaguars have been shown to prefer forests and avoid anthropogenic and open habitats within ecoregions,^{11,12} the factors associated with the spatial needs and movements of jaguars across the habitat types that it inhabits have not been examined. Using data from 111 jaguars from 13 ecoregions, across 24 sites within the four

Luis D. Alfaro,²² Isabel Hagnauer,²⁸ Marina Xavier da Silva,²⁹ Alexandre Vogliotti,³⁰ Marcela F.D. Moraes,²⁹ Selma S. Miyazaki,¹⁵ Gediendson R. Araujo,^{31,32} Leanes Cruz da Silva,^{32,33} Lucas Leuzinger,³² Marina M. Carvalho,³⁴ Lilian Rampim,¹⁷ Leonardo Sartorello,¹⁷ Howard Quigley,¹⁸ Fernando R. Tortato,¹⁸ Rafael Hoogesteijn,¹⁸ Peter G. Crawshaw Jr.,³ Allison L. Devlin,^{18,35,36} Joares A. May Júnior,^{5,17,18,37} George V.N. Powell,³⁸ Mathias W. Tobler,³⁹ Samia E. Carrillo-Percastegui,³⁹ Estebán Payán,¹⁸ Fernando C.C. Azevedo,^{5,40} Henrique V.B. Concone,^{5,41} Verónica A. Quiroga,^{9,42,43} Sebastián A. Costa,^{8,9} Juan P. Arrabal,^{9,44} Ezequiel Vanderhoeven,^{9,44} Yamil E. Di Blanco,^{8,9} Alexandre M.C. Lopes,⁴⁵ and Milton Cezar Ribeiro⁴

¹⁴Instituto Onça Pintada, Mineiros, GO 75830000, Brazil

¹⁵Estacao Ecológica Taiamã, Instituto Chico Mendes de Conservação da Biodiversidade, Cáceres, MT 78210625, Brazil

¹⁶Instituto de Desenvolvimento Sustentável Mamirauá, Tefé, AM 69553225, Brazil

¹⁷Associação Onçafari, Rua Ferreira de Araújo, 221, Cj.14, Sala 4, Pinheiros, São Paulo, SP 05428-000, Brazil

¹⁸Panthera, 8 West 40th Street, 18th Floor, New York, NY 10018, USA

¹⁹Instituto SOS Pantanal, R. Gutemberg, 328 Centro, Campo Grande, MS 79002-160, Brazil

²⁰Programa de Pós-graduação em Biologia Animal, Instituto de Biociências, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, RS 91501970, Brazil

²¹Instituto de Ecología, Universidad Nacional Autónoma de México and CONACyT, Ciudad Universitaria, México D.F. 04318, México

²²Instituto Internacional en Conservación y Manejo de Vida Silvestre, Universidad Nacional de Costa Rica, Heredia 1350-3000, Costa Rica

²³Department of Environmental Conservation, University of Massachusetts, Amherst, Amherst, MA 01003, USA

²⁴Centro de Investigación en Ciencias Biológicas Aplicadas, Universidad Autónoma del Estado de México, Instituto Literario 100, Col. Centro C.P. 50000, Toluca, Estado de México

²⁵Instituto de Biologia, Laboratório de Ecologia de Mamíferos LEMA, Universidade Federal de Uberlândia, Uberlândia, MG 38408100, Brazil

²⁶Primero Conservation, Box 1588, Pinetop, AZ 85935, USA

²⁷Namá Conservation, Heredia 40101, Costa Rica

²⁸Rescate Animal Zooave, Fundación Restauración de la Naturaleza, Apdo 1327-4050, Alajuela, Costa Rica

²⁹Projeto Carnívoros do Iguaçu, Foz do Iguaçu, PR 85851970, Brazil

³⁰Universidade Federal da Integração Latino-Americana, Instituto Latino-Americano de Ciências da Vida e da Natureza, Foz do Iguaçu, PR 85851970, Brazil

³¹Universidade Federal de Mato Grosso do Sul, Faculdade de Medicina Veterinária e Zootecnia, Campo Grande, MS 79070-900, Brazil

³²Instituto Onças do Rio Negro, Fazenda Barranco Alto, Aquidauana, MS 79208000, Brazil

³³Departamento de Medicina Veterinária, Universidade Federal de Viçosa, Viçosa, MG 36570, Brazil

³⁴Instituto de Defesa e Preservação dos Felídeos Brasileiros, Corumbá de Goiás, GO 72960000, Brazil

³⁵SUNY College of Environmental Science & Forestry, Syracuse, NY 13210, USA

³⁶Wildlife Biology Program, W.A. Franke College of Forestry & Conservation, University of Montana, Missoula, MT 59812, USA

³⁷Universidade do Sul de Santa Catarina, Tubarão, SC 88704-900, Brazil

³⁸Wildlife Protection Solutions, 2501 Welton Street, Denver, CO 80205, USA

³⁹San Diego Zoo Global, Institute for Conservation Research, 15600 San Pasqual Valley Road, Escondido, CA 92027, USA

⁴⁰Universidade Federal de São João del Rei, Departamento de Ciências Naturais, São João del Rei, MG 36301160, Brazil

⁴¹Laboratório de Ecologia, Manejo e Conservação de Fauna Silvestre, Programa de Pós-Graduação Interunidades em Ecologia Aplicada, Universidade de São Paulo ESALQ/CENA, Piracicaba, SP 13418-900, Brazil

⁴²Universidad Nacional de Córdoba, Facultad de Ciencias Exactas, Físicas y Naturales, Centro de Zoología Aplicada, Córdoba, Argentina

⁴³Consejo Nacional de Investigaciones Científicas y Técnicas CONICET, Instituto de Diversidad y Ecología Animal IDEA, Córdoba, Argentina

⁴⁴Instituto Nacional de Medicina Tropical ANLIS, Ministerio de Salud de la Nación, Puerto Iguazú, Misiones 3370, Argentina

⁴⁵Instituto de Pesquisa e Conservação de Tamanduás do Brasil, Parnaíba, PI 64200025, Brazil

⁴⁶Twitter: @DrJJThompson

⁴⁷Lead contact

*Correspondence: jthompson.py@gmail.com

<https://doi.org/10.1016/j.cub.2021.06.029>

biomes that constitute almost all of the jaguar's current distribution,^{9,13} we examined the relationships among environmental and anthropogenic factors with home range size and movement parameters toward identifying commonalities across the jaguar's distribution (Figure 1).

Home range and movement parameter estimates

All individuals demonstrated range residency, with their movements best characterized by the Ornstein–Uhlenbeck or Ornstein–Uhlenbeck with foraging models (with or without correlated velocity and position autocorrelation timescales).¹⁴ The 95% home range areas ranged between 35.2 and 2,914.9 km² for males and 13.4 and 1,154.8 km² for females (Table S1). Velocity autocorrelation timescale, which is the average time period over which an individual moves in the same direction and at the

same speed across time lags, and is a measure of tortuosity (lower values equate to higher tortuosity),^{14,15} ranged between 0.08 and 8.05 h and 0.03 and 3.6 h for males and females, respectively, and speed ranged between 3.4 and 30.4 km/day for males and 2.9 and 23.2 km/day for females (Table S1). We tested for correlation among estimates using Pearson's correlation coefficient and found no correlation of home range area with speed ($r = 0.19$) or velocity autocorrelation timescale ($r = 0.03$) or between speed and velocity autocorrelation timescale ($r = -0.42$).

Factors associated with home range size and movement parameters

The highest ranking model set for home range size contained four parameters, all of which were informative (Tables S2 and S3): percent forest cover and net primary productivity were

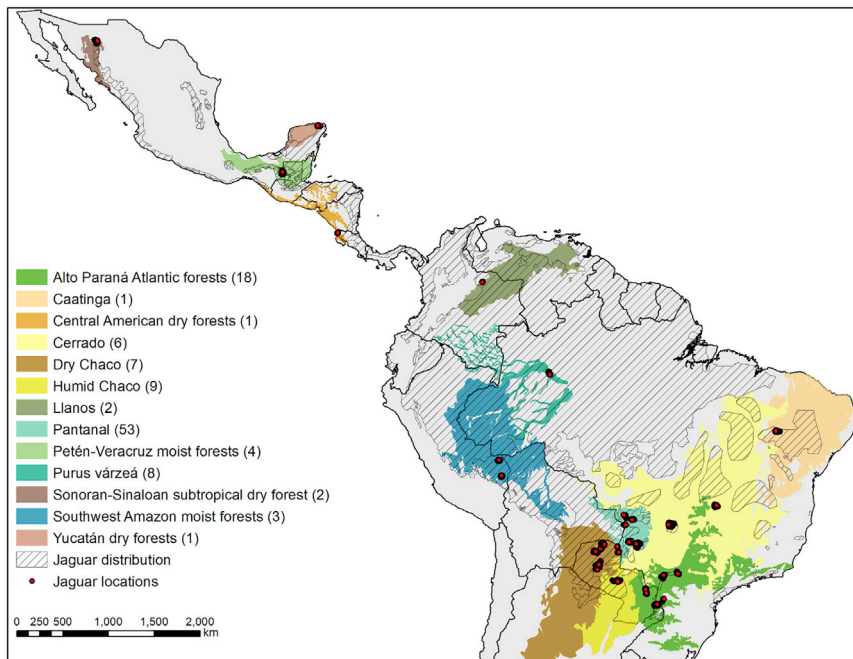


Figure 1. Telemetry data locations

Locations in North and South America by ecoregion¹³ of telemetered jaguars included in the analysis. Numbers next to ecoregions represent the number of telemetry datasets per ecoregion. See also [Table S1](#).

and forest cover or with lower road densities, such as the eastern slope of the Andes and portions of the Pantanal, Llanos, Amazon Basin, Atlantic forest, and humid Mesoamerican forests, had the smallest predicted relative home range size ([Figure 4](#)).

It would be expected that if the differences in our predicted home range sizes across ecoregions are representative of jaguar spatial needs, there should be a general correlation between home range size with densities.¹⁶ To test this, we compared density estimates from our study ecoregions^{17–28} with mean estimates of home range size for our study

negatively associated with home range size, and road density and sex (male) were positively associated. Based upon the posterior distributions of the parameter estimates, males had a 100% probability of having larger home ranges than females ([Table S4](#)), while percent forest cover and net primary productivity had a 98% and 91% probability, respectively, of being related with smaller home range size, and road density had a 100% probability of being related to increased home range size ([Figure 2](#); [Table S4](#)). Importantly, net primary productivity had a stronger effect than the other landscape covariates on home range size, with a 1.4–1.9 times greater mean effect than other covariates ([Figure 2](#); [Table S4](#)).

Speed was inversely related to percent forest cover, with a 100% probability of being related to decreasing speed, and there was no difference in speed between sexes ([Figure 2](#); [Table S4](#)). No landscape covariates were associated with the velocity autocorrelation timescale, although males had 100% probability of having a greater velocity autocorrelation timescale than females ([Figure 2](#); [Table S4](#)).

Using the parameter estimates from the home range model and the landscape covariates, we spatially predicted home range size within the intersection of the jaguars' distribution and our study ecoregions ([Figure 3](#)). We also mapped the predicted relative home range size across the jaguars' distribution based upon the mean ecoregion effect (ecoregion hyperparameter) and landscape covariates ([Figure 4](#)). Home range predictions within ecoregions varied spatially in all ecoregions; however, the variation was most evident in the ecoregions outside of the Amazon that had greater variation in forest cover (natural or anthropogenically caused) and a greater occurrence of roads ([Figure 3](#)). Across the jaguars' distribution, areas with lower productivity and forest cover or higher road density such as the Caatinga, Cerrado, Dry Chaco, Central America and Mexican dry forests, and the Caribbean slope of Colombia were predicted to have larger home ranges ([Figure 4](#)). Conversely, systems with high productivity

ecoregions ([Figure S1](#); [Table S5](#)), finding a correlation ($r = -0.70$) between smaller home range size and higher jaguar densities in productive systems such as the Pantanal, Llanos, and southwestern Amazon, and lower densities and larger home ranges in semi-arid ecoregions with lower productivity and forest cover, including the Caatinga, Cerrado, Sonoran-Sinaloan subtropical dry forest, and Dry Chaco.

DISCUSSION

Home range size

The positive relationship of home range size with increasing road density and negative relationship with increasing forest cover and ecosystem productivity are consistent with research on jaguar spatial ecology and distribution^{10–12,29,30} and patterns in terrestrial carnivore space use.^{16,31–34} For several ecoregions, however, sample sizes were low and, subsequently, our ecoregion-specific results need to be interpreted within the context of the associated uncertainty.

Decreasing home range size in relation to increasing forest cover and ecosystem productivity is attributable to greater availability of preferred habitat and prey, which reduces spatial needs to meet metabolic and reproductive requirements.^{16,32,34} Increasing road density can affect jaguars and other large cats^{33,35–41} through direct human mortality (hunting, vehicle collisions) or through prey reduction, while driving behavioral changes related to human presence and land use to avoid or use areas of greater risk, which increases costs to movements and increases spatial needs. We recognize that greater forest cover and net primary productivity do not necessarily translate to greater prey availability since in tropical humid forests in particular, biomass is concentrated in the canopy,^{42,43} which in part explains jaguars' association with rivers in these systems^{11,44} and the relatively large estimated home ranges in the Southwest Amazon and Petén-Veracruz moist

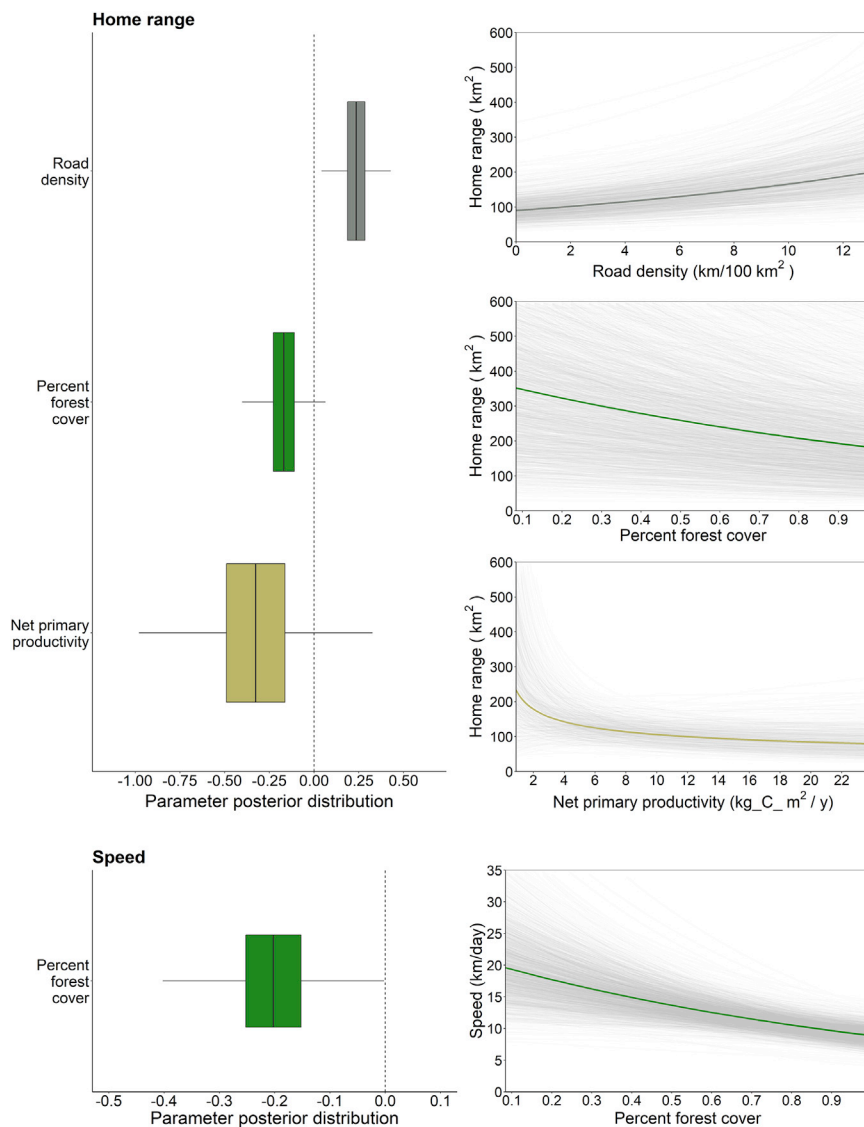


Figure 2. Ecoregional scale relationships of home range size with covariates

Left: posterior distributions of the parameter estimates from the Bayesian analysis of the generalized linear mixed model with ecoregion as a random effect for home range size and speed. Boxplots represent the median and 25th and 75th quantiles and whiskers 1.5 times the upper and lower interquartile range, with the dashed line representing the value of no effect upon the movement parameter by the covariate. Right: estimated responses of home range size and speed to landscape covariates. Colored lines represent mean effect and gray lines are 1,000 estimated responses based upon random draws from the parameter posterior distributions. See also [Tables S4](#) and [S6](#).

and the need to maintain reproductive opportunities by maximizing their contact with females. In contrast, females have smaller home ranges to minimize metabolic costs while maximizing food availability and reproductive success.^{60,61}

Movement parameters

Speed was solely related to forest cover, decreasing with increasing forest cover, and did not differ between sexes, while directionality of movements was not related to any of the covariates but was greater for males. For speed, this indicates that decisions about movement at the home range scale were dependent upon the availability of preferred habitat and that jaguars adjust their behavior to account for anthropogenic factors.^{11,12,62–65}

Animal movements are expected to be slower in areas of higher habitat quality and reduced habitat heterogeneity and fragmentation,^{66,67} which has been observed in big cats,^{68–71} and consequently, the inverse relationship between speed and forest cover is expected given jaguars' preference for forest cover.^{11,12,64,65}

Mean speed was similar between sexes, but male movements were more directional, which is logical given that male home ranges are larger, and to be traversed at the same speed as females, movements would have to be less tortuous. Directionality of movements was not related to landscape-scale factors suggesting that jaguars are responding to more local factors in their finer-scale movement decisions; however, female movements were more tortuous. The greater tortuosity observed in females implies sex-based differences in response to fine-scale environmental and anthropogenic habitat characteristics as have been observed in other large cats.^{55,70,72–75} Thus, female displacement is lower than for males, despite having similar movement rates, which shows the potential error that can occur when estimating distance traveled from non-linear movement paths based upon linear displacements.⁷⁶

forest where forest cover and productivity are comparatively high ([Table S5](#)).

Although local-scale factors can affect jaguar densities, and we have shown that multiple opposing factors shape jaguar spatial needs, there was a correlation between home range size and densities within our study ecoregions ([Figure S1](#)) as would be expected based upon energetic limits.¹⁶ Similarly, the relationship between densities in other regions^{41,45–49} and home range size is evident in the range-wide predictions of our model ([Figure 4](#)) where increasing estimated densities corresponded to increasing predicted relative home range size. However, as our predictions are based upon mean predicted effects, their representation of areas for which we did not have data needs to be interpreted cautiously, especially for humid forests, given the aforementioned potential bias stemming from the availability of terrestrial prey biomass in these systems.

Larger home range size in males was expected based upon previous research on jaguars^{29,50–52} and other large felids^{53–59} since male home range size is driven by both food availability

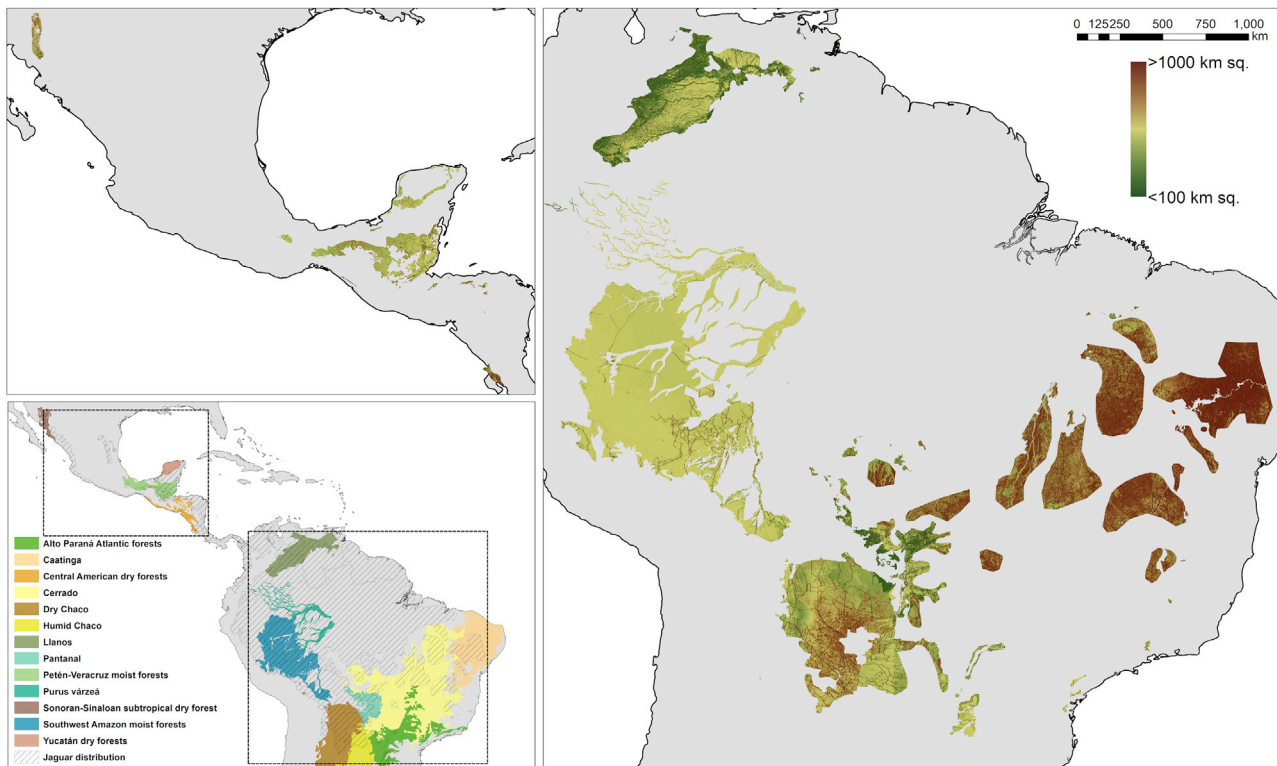


Figure 3. Predicted mean jaguar home range size within study ecoregions

Predicted mean home range size for jaguars within study ecoregions within the jaguars' distribution based upon ecoregion-specific model intercepts from the home range model and the corresponding landscape-scale covariates. See also [Figure S1](#) and [Tables S4–S6](#).

Consequently, observed anthropogenically driven reductions in mammalian displacements, at least in jaguars, may not be due to reduced movement,⁶² but rather greater tortuosity in movements.²⁹

Implications

Our dataset and analysis are the largest to date on the movement ecology of the jaguar, or for any large felid, spanning its complete extant range, representing the spectrum of habitat types that jaguars inhabit and varying levels of anthropogenic transformation. We demonstrated that the anthropogenic and environmental factors affecting jaguar space use and movement at local and regional scales^{11,12,64,65} act similarly across ecoregions to affect jaguar spatial needs and movements, demonstrating that jaguars tend to perceive their environment similarly, regardless of geographic location or habitat type. Importantly, we illustrated that ecosystem productivity, forest cover, and the presence of roads strongly drive jaguar home range size throughout the species distribution, which is consistent with observed behavior of jaguars^{10,11,30,41,63} and other felids,^{35,39,77} and with expectations across terrestrial mammalian carnivores in general.^{16,32}

We demonstrate that jaguars adjust their behavior in relation to differences in environmental and anthropogenic factors as observed at more local scales^{11,63–65} and in other large cat species.^{68,69,72,75,77–80} This has applications for the conservation of the jaguar as we provide a set of landscape metrics and a

mechanism to evaluate jaguar habitat quality throughout the species' range. Although our analysis infers strong relationships between jaguar spatial needs and landscape-level variables, the relationship between most of those variables and movements within home ranges is less clear, pointing to a need to understand the ultimate factors determining finer-scale movement decisions and the behavioral adaptability of jaguar to differences in habitat quality.

Some large cats, such as the puma and leopard, are capable of modifying their behavior in response to anthropogenic influences to persist in highly modified landscapes,^{37,72,74,75,80,81} which is not surprising given the adaptability of both species indicated by their large multi-continental distributions across both temperate and tropical ecosystems.^{82,83} Interestingly, in highly anthropogenic landscapes, home range size of pumas and leopards contracted instead of increased, as we found with jaguar in relation to road density. This pattern of home range constriction might not be evident for the jaguar since, despite being eclectic and adaptable in its diet,⁸⁴ the jaguar is less of a habitat generalist than the puma and leopard, and may be subject to greater mortality in anthropogenic landscapes, and is consequently extirpated from more anthropized regions despite suitable habitat and prey availability.^{50,85,86}

In highly transformed landscapes where jaguars persist, however, there is evidence that jaguars make behavioral adjustments that reduce their space use. Jaguars in the Atlantic forest showed high fidelity to protected areas, decreasing home range



Figure 4. Predicted relative range-wide jaguar home range size

Predicted relative mean home range sizes for jaguars across its distribution⁹ based upon ecoregion hyperparameter and mean parameter effects for the landscape-scale covariates from the home range model and corresponding landscape-scale covariates. As these predictions are based upon mean effects, they need to be interpreted within the context of the associated uncertainties in model parameter estimates. See also [Tables S4](#) and [S6](#).

size in relation to decreases in the size of protected areas; reduced sexual differences in home range size; and showed no relationship between home range size and landscape-scale anthropogenic factors.^{20,87} Also, jaguars have been shown to greatly decrease space use in highly modified areas with relatively high human population density when supplemental food was available.⁸⁸ When placed within the context of our results, these observations illustrate behavioral plasticity by jaguars, and given the extensive retraction in the jaguars' distribution due to anthropogenic factors and the number of threatened populations,⁵ highlights the need for additional research to understand jaguars' tolerance of land use and human presence for developing effective conservation actions.

Our analysis is unique in that it is the first to elucidate the factors related to space use and movements by a terrestrial apex predator across its distribution and the principle habitat types that it inhabits, which is of consequence since understanding how organisms perceive their environment is essential for understanding their ecology and behavior,⁸⁹ especially for carnivores,⁹⁰ while home ranges are a manifestation of organisms'

movements in space and time in response to heterogeneity in their environment.^{62,91} Given the geographic and ecological breadth of our analysis, and its accounting for uncertainty from relatively small sample sizes typical of large carnivore research, our inferences not only provide robust generalizations that address key needs for the jaguars' range-wide conservation,⁶ but also for the conservation of other large cats,^{92–94} and large terrestrial carnivores in general.²

By demonstrating the large-scale factors associated with jaguar spatial needs, we provide a set of landscape metrics to evaluate jaguar habitat quality throughout the species' range, facilitating transboundary conservation planning among jaguar range states, which is of significance as the range-wide conservation vision for the jaguar is based upon international collaboration and trans-boundary decision making to maintain connectivity among core jaguar populations (Jaguar Conservation Units).⁶ Moreover, given that habitat loss, human population growth, and road intrusion are common threats to large cat conservation,^{2,5,82,95–97} our modeling framework is useful to identify the environmental and anthropogenic factors associated with

large cat and other large carnivore spatial needs for assessing habitat suitability and to guide conservation and reintroduction decisions.³² Therefore, our findings and analysis framework have immediate and direct applications for the range-wide conservation of jaguars, other large cats, and large terrestrial carnivores around the world and the biodiversity for which they are proxy.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
 - Lead Contact
 - Materials Availability
 - Data and Code Availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
 - Ethics statement
- METHOD DETAILS
 - Telemetry data
 - Covariates
- QUANTIFICATION AND STATISTICAL ANALYSIS
 - Workflow
 - Home range and movement parameter estimation
 - Model selection and specification

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2021.06.029>.

ACKNOWLEDGMENTS

J.J.T. was partly supported by CONACYT of Paraguay through the program PRONII. Additional support was provided by the Fazenda Real Filial São Bento, the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil CAPES – Finance Code 001, Fundação de Amparo à Pesquisa do Estado de São Paulo 2018/13037–3, FAPESP 2014/24921–0, FAPESP 2018/24891–5, FAPESP 2014/24921–0, CONICET, CelBA, WWF Switzerland, Fundación Vida Silvestre Argentina, Panthera Foundation, and Rufford Small Grant Foundation. We appreciate the valuable inputs of John Polisar to the development of our manuscript. We would like to dedicate this article to the memory of our coauthor Dr. Peter G. Crawshaw Jr., a pioneer in jaguar movement ecology and jaguar conservation in Brazil.

AUTHOR CONTRIBUTIONS

J.J.T., R.G.M., B.B.N., A.P., and J.A.T. conceptualized the analysis; J.J.T., B.B.N., V.B.A., J.E.F.O., and A.E.B. undertook the analysis; J.J.T., R.G.M., and B.B.N. led the writing of the manuscript; and J.J.T., R.G.M., B.B.N., A.P., J.A.T., F.L., R.T.M., R.C.P., L.C., L. Silveira, D.L.Z.K., E.E.R., L.M., M.H., D.A.S., R.A.M., E.C., V.H.M., O.M.-V., P.C., A.T.A.J., G.B.A., I.C., R.T., C.S.-B., J.C.C., L.D.A., I.H., M.X.S., A.V., M.F.D.M., S.S.M., G.R.A., L.C.S., L.L., M.M.C., L.R., L. Sartorello, H.Q., F.R.T., R.H., P.G.C., A.L.D., J.A.M.J., G.V.N.P., S.E.C.-P., E.P., F.C.C.A., H.V.B.C., V.A.Q., S.A.C., J.P.A., E.V., Y.E.D.B., A.M.C.L., and M.C.R. provided data. All authors contributed to the writing.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: October 28, 2020

Revised: March 4, 2021

Accepted: June 10, 2021

Published: July 7, 2021

REFERENCES

1. Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., and Collen, B. (2014). Defaunation in the Anthropocene. *Science* 345, 401–406.
2. Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., et al. (2014). Status and ecological effects of the world's largest carnivores. *Science* 343, 1241484.
3. Ceballos, G., Ehrlich, P.R., and Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl. Acad. Sci. USA* 114, E6089–E6096.
4. Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., et al. (2011). Trophic downgrading of planet Earth. *Science* 333, 301–306.
5. de la Torre, J.A., González-Maya, J.F., Zarza, H., Ceballos, G., and Medellín, R.A. (2018). The jaguar's spots are darker than they appear: assessing the global conservation status of the jaguar *Panthera onca*. *Oryx* 52, 300–315.
6. United Nations Development Program; Panthera; Wildlife Conservation Society; Worldwide Fund for Nature (2019). Jaguar 2030 Roadmap. Regional plan to save America's largest cat and its ecosystem. https://www.panthera.org/cms/sites/default/files/Panthera_Jaguar2030Roadmap_ENG.pdf.
7. Rabinowitz, A. (2014). *An Indomitable Beast* (Island Press).
8. Rabinowitz, A., and Zeller, K.A. (2010). A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. *Biol. Conserv.* 143, 939–945.
9. Quigley, H., Foster, R., Petracca, L., Payan, E., Salom, R., and Harmsen, B. (2017). *Panthera onca*. <http://www.iucnredlist.org/details/15953/0>.
10. Jędrzejewski, W., Robinson, H.S., Abarca, M., Zeller, K.A., Velasquez, G., Paemelaere, E.A.D., Goldberg, J.F., Payan, E., Hoogesteijn, R., Boede, E.O., et al. (2018). Estimating large carnivore populations at global scale based on spatial predictions of density and distribution – Application to the jaguar (*Panthera onca*). *PLoS ONE* 13, e0194719.
11. Morato, R.G., Connette, G.M., Stabach, J.A., De Paula, R.C., Ferraz, K.M.P.M., Kantek, D.L.Z., Miyazaki, S.S., Pereira, T.D.C., Silva, L.C., Paviolo, A., et al. (2018). Resource selection in an apex predator and variation in response to local landscape characteristics. *Biol. Conserv.* 228, 233–240.
12. Costa Alvarenga, G., Chiaverini, L., Cushman, S.A., Dröge, E., Macdonald, D.W., Kantek, D.L.Z., Morato, R.G., Thompson, J.J., Oscar, R.B.L.M., Abade, L., et al. (2021). Multi-scale path-level analysis of jaguar habitat use in the Pantanal ecosystem. *Biol. Conserv.* 253, 108900.
13. Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., et al. (2001). Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience* 51, 933.
14. Fleming, C.H., Calabrese, J.M., Mueller, T., Olson, K.A., Leimgruber, P., and Fagan, W.F. (2014). From fine-scale foraging to home ranges: a semivariance approach to identifying movement modes across spatio-temporal scales. *Am. Nat.* 183, E154–E167.
15. Gurarie, E., Bracis, C., Delgado, M., Meckley, T.D., Kojola, I., and Wagner, C.M. (2016). What is the animal doing? Tools for exploring behavioural structure in animal movements. *J. Anim. Ecol.* 85, 69–84.
16. Carbone, C., and Gittleman, J.L. (2002). A common rule for the scaling of carnivore density. *Science* 295, 2273–2276.
17. Soisalo, M.K., and Cavalcanti, S.M.C. (2006). Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and

- capture–recapture sampling in combination with GPS radio-telemetry. *Biol. Conserv.* **129**, 487–496.
18. Jędrzejewski, W., Puerto, M.F., Goldberg, J.F., Hebblewhite, M., Abarca, M., Gamarra, G., Calderón, L.E., Romero, J.F., Vilorio, Á.L., Carreño, R., et al. (2017). Density and population structure of the jaguar (*Panthera onca*) in a protected area of Los Llanos, Venezuela, from 1 year of camera trap monitoring. *Mammal Res.* **62**, 9–19.
 19. Boron, V., Tzanopoulos, J., Gallo, J., Barragan, J., Jaimes-Rodriguez, L., Schaller, G., and Payán, E. (2016). Jaguar densities across human-dominated landscapes in Colombia: the contribution of unprotected areas to long term conservation. *PLoS ONE* **11**, e0153973.
 20. Paviolo, A., De Angelo, C., Ferraz, K.M.P.M.B., Morato, R.G., Martinez Pardo, J., Srbek-Araujo, A.C., Beisiegel, B.M., Lima, F., Sana, D., Xavier da Silva, M., et al. (2016). A biodiversity hotspot losing its top predator: the challenge of jaguar conservation in the Atlantic Forest of South America. *Sci. Rep.* **6**, 37147.
 21. Tobler, M.W., Carrillo-Percastegui, S.E., Zúñiga Hartley, A., and Powell, G.V.N. (2013). High jaguar densities and large population sizes in the core habitat of the southwestern Amazon. *Biol. Conserv.* **159**, 375–381.
 22. Sollmann, R., Furtado, M.M., Gardner, B., Hofer, H., Jácomo, A.T.A., Tôrres, N.M., and Silveira, L. (2011). Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. *Biol. Conserv.* **144**, 1017–1024.
 23. Silveira, L., Jácomo, A.T.A., Astete, S., Sollmann, R., Tôrres, N.M., Furtado, M.M., and Marinho-Filho, J. (2010). Density of the near threatened jaguar *Panthera onca* in the caatinga of north-eastern Brazil. *Oryx* **44**, 104–109.
 24. Noss, A.J., Gardner, B., Maffei, L., Cuéllar, E., Montaña, R., Romero-Muñoz, A., Sollman, R., and O’Connell, A.F. (2012). Comparison of density estimation methods for mammal populations with camera traps in the Kaa-lya del Gran Chaco landscape: density estimation with camera traps in the Chaco. *Anim. Conserv.* **15**, 527–535.
 25. Gutiérrez-González, C.E., Gómez-Ramírez, M.Á., and López-González, C.A. (2012). Estimation of the density of the Near Threatened jaguar *Panthera onca* in Sonora, Mexico, using camera trapping and an open population model. *Oryx* **46**, 431–437.
 26. Finnegan, S.P., Galvez-Bravo, L., Silveira, L., Tôrres, N.M., Jácomo, A.T.A., Alves, G.B., and Dalerum, F. (2020). Reserve size, dispersal and population viability of wide ranging carnivores: the case of jaguars in Emas National Park, Brazil. *Anim. Conserv.* **24**, 3–14.
 27. Greenspan, E., Anile, S., and Nielsen, C.K. (2020). Density of wild felids in Sonora, Mexico: a comparison of spatially explicit capture–recapture methods. *Eur. J. Wildl. Res.* **66**, 60.
 28. Ávila-Nájera, D.M., Chávez, C., Lazcano-Barrero, M.A., Pérez-Elizalde, S., and Alcántara-Carbajal, J.L. (2015). Estimación poblacional y conservación de felinos (Carnivora: Felidae) en el norte de Quintana Roo, México. *Rev. Biol. Trop.* **63**, 799–813.
 29. Morato, R.G., Stabach, J.A., Fleming, C.H., Calabrese, J.M., De Paula, R.C., Ferraz, K.M.P.M., Kantek, D.L.Z., Miyazaki, S.S., Pereira, T.D.C., Araujo, G.R., et al. (2016). Space use and movement of a neotropical top predator: the endangered Jaguar. *PLoS ONE* **11**, e0168176.
 30. Colchero, F., Conde, D.A., Manterola, C., Chávez, C., Rivera, A., and Ceballos, G. (2011). Jaguars on the move: modeling movement to mitigate fragmentation from road expansion in the Mayan Forest: modeling jaguar movement to locate wildlife passes. *Anim. Conserv.* **14**, 158–166.
 31. Crooks, K.R. (2002). Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conserv. Biol.* **16**, 488–502.
 32. Nilsen, E.B., Herfindal, I., and Linnell, J.D.C. (2005). Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? *Ecoscience* **12**, 68–75.
 33. Woodroffe, R. (2000). Predators and people: using human densities to interpret declines of large carnivores. *Anim. Conserv.* **3**, 165–173.
 34. Fuller, T.K., and Sievert, P.R. (2001). Carnivore demography and the consequences of changes in prey availability. In *Carnivore Conservation*, J.L. Gittleman, S. Funk, D. McDonald, and R.K. Wayne, eds. (Press Syndicate of the University of Cambridge), pp. 163–178.
 35. Kerley, L.L., Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Quigley, H.B., and Hornocker, M.G. (2002). Effects of roads and human disturbance on amur tigers. *Conserv. Biol.* **16**, 97–108.
 36. Linkie, M., Chapron, G., Martyr, D.J., Holden, J., and Leader-Williams, N. (2006). Assessing the viability of tiger subpopulations in a fragmented landscape. *J. Appl. Ecol.* **43**, 576–586.
 37. Kertson, B.N., Spencer, R.D., Marzluff, J.M., Hepinstall-Cymerman, J., and Grue, C.E. (2011). Cougar space use and movements in the wildland–urban landscape of western Washington. *Ecol. Appl.* **21**, 2866–2881.
 38. Abade, L., Cusack, J., Moll, R.J., Strampelli, P., Dickman, A.J., Macdonald, D.W., and Montgomery, R.A. (2020). The relative effects of prey availability, anthropogenic pressure and environmental variables on lion (*Panthera leo*) site use in Tanzania’s Ruaha landscape during the dry season. *J. Zool. (Lond.)* **310**, 135–144.
 39. Dickson, B.G., and Beier, P. (2002). Home-range and habitat selection by adult cougars in Southern California. *J. Wildl. Manage.* **66**, 1235.
 40. Henschel, P., Hunter, L.T.B., Coad, L., Abernethy, K.A., and Mühlenberg, M. (2011). Leopard prey choice in the Congo Basin rainforest suggests exploitative competition with human bushmeat hunters: leopard prey choice in the Congo Basin. *J. Zool. (Lond.)* **285**, 11–20.
 41. Espinosa, S., Celis, G., and Branch, L.C. (2018). When roads appear jaguars decline: increased access to an Amazonian wilderness area reduces potential for jaguar conservation. *PLoS ONE* **13**, e0189740.
 42. Polisar, J., Maxit, I., Scognamiglio, D., Farrell, L., Sunquist, M.E., and Eisenberg, J.F. (2003). Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. *Biol. Conserv.* **109**, 297–310.
 43. Kays, R., and Allison, A. (2001). Arboreal tropical forest vertebrates: current knowledge and research trends. In *Tropical Forest Canopies: Ecology and Management Forestry Sciences*, K.E. Linsenmair, A.J. Davis, B. Fiala, and M.R. Speight, eds. (Springer Netherlands), pp. 109–120.
 44. Emmons, L.H. (1987). Comparative feeding ecology of felids in a neotropical rainforest. *Behav. Ecol. Sociobiol.* **20**, 271–283.
 45. Harmsen, B.J., Foster, R.J., and Quigley, H. (2020). Spatially explicit capture recapture density estimates: robustness, accuracy and precision in a long-term study of jaguars (*Panthera onca*). *PLoS ONE* **15**, e0227468.
 46. Hidalgo-Mihart, M.G., Jesús-de la Cruz, A., Contreras-Moreno, F.M., Juárez-López, R., Bravata-de la Cruz, Y., Friedeberg, D., and Bautista-Ramírez, P. (2019). Jaguar density in a mosaic of disturbed/preserved areas in southeastern Mexico. *Mamm. Biol.* **98**, 173–178.
 47. Lavariega, M.C., Ríos-Solis, J.A., Flores-Martínez, J.J., Galindo-Aguilar, R.E., Sánchez-Cordero, V., Juan-Albino, S., and Soriano-Martínez, I. (2020). Community-based monitoring of jaguar (*Panthera onca*) in the Chinantla Region, Mexico. *Trop. Conserv. Sci.* **13**, 194008292091782.
 48. Mena, J.L., Yagui, H., Tejada, V., Cabrera, J., Pacheco-Esquivel, J., Rivero, J., and Pastor, P. (2020). Abundance of jaguars and occupancy of medium- and large-sized vertebrates in a transboundary conservation landscape in the northwestern Amazon. *Glob. Ecol. Conserv.* **23**, e01079.
 49. Petit, M., Denis, T., Rux, O., Richard-Hansen, C., and Berzins, R. (2018). Estimating jaguar (*Panthera onca*) density in a preserved coastal area of French Guiana. *Mammalia* **82**, 188–192.
 50. McBride, R.T., and Thompson, J.J. (2018). Space use and movement of jaguar (*Panthera onca*) in western Paraguay. *Mammalia* **82**, 540–549.
 51. de La Torre, J.A., and Rivero, M. (2019). Insights of the movements of the jaguar in the tropical forests of southern Mexico. In *Movement Ecology of Neotropical Forest Mammals*, R. Reyna-Hurtado, and C.A. Chapman, eds. (Springer Nature), pp. 217–242.

52. de la Torre, J.A., Núñez, J.M., and Medellín, R.A. (2017). Spatial requirements of jaguars and pumas in Southern Mexico. *Mamm. Biol.* *84*, 52–60.
53. Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Kerley, L.L., Quigley, H.B., and Hornocker, M.G. (2010). Spatial structure of Amur (Siberian) tigers (*Panthera tigris altaica*) on Sikhote-Alin Biosphere Zapovednik, Russia. *J. Mammal.* *91*, 737–748.
54. Hernandez-Blanco, J.A., Naidenko, S.V., Chistopolova, M.D., Lukarevskiy, V.S., Kostyrya, A., Rybin, A., Sorokin, P.A., Litvinov, M.N., Kotlyar, A.K., Miquelle, D.G., and Rozhnov, V.V. (2015). Social structure and space use of Amur tigers (*Panthera tigris altaica*) in Southern Russian Far East based on GPS telemetry data. *Integr. Zool.* *10*, 365–375.
55. Johansson, Ö., Koehler, G., Rauset, G.R., Samelius, G., Andrén, H., Mishra, C., Lhagvasuren, P., McCarthy, T., and Low, M. (2018). Sex-specific seasonal variation in puma and snow leopard home range utilization. *Ecosphere* *9*, e02371.
56. Mizutani, F., and Jewell, P.A. (1998). Home-range and movements of leopards (*Panthera pardus*) on a livestock ranch in Kenya. *J. Zool. (Lond.)* *244*, 269–286.
57. Grigione, M.M., Beier, P., Hopkins, R.A., Neal, D., Padley, W.D., Schonewald, C.M., and Johnson, M.L. (2002). Ecological and allometric determinants of home-range size for mountain lions (*Puma concolor*). *Anim. Conserv.* *5*, 317–324.
58. Loveridge, A.J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H., and Macdonald, D.W. (2009). Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography* *32*, 953–962.
59. Tumenta, P.N., van't Zelfde, M., Croes, B.M., Buij, R., Funston, P.J., Udo de Haes, H.A., and De Iongh, H.H. (2013). Changes in lion (*Panthera leo*) home range size in Waza National Park, Cameroon. *Mamm. Biol.* *78*, 461–469.
60. Sandell, M. (1989). The mating tactics and spacing patterns of solitary carnivores. In *Carnivore Behavior, Ecology, and Evolution*, J.L. Gittleman, ed. (Springer), pp. 164–182.
61. Sunquist, M.E., and Sunquist, F.C. (1989). Ecological constraints on predation by large felids. In *Carnivore Behavior, Ecology, and Evolution*, J.L. Gittleman, ed. (Springer), pp. 283–301.
62. 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.
63. Conde, D.A., Colchero, F., Zarza, H., Christensen, N.L., Sexton, J.O., Manterola, C., Chávez, C., Rivera, A., Azuara, D., and Ceballos, G. (2010). Sex matters: Modeling male and female habitat differences for jaguar conservation. *Biol. Conserv.* *143*, 1980–1988.
64. Kanda, C.Z., Oliveira-Santos, L.G.R., Morato, R.G., de Paula, R.C., Rampim, L.E., Sartorello, L., Haberkfeld, M., Galetti, M., and Cezar Ribeiro, M. (2019). Spatiotemporal dynamics of conspecific movement explain a solitary carnivore's space use. *J. Zool. (Lond.)* *308*, 66–74.
65. Cullen, L., Junior, Sana, D.A., Lima, F., de Abreu, K.C., and Uezu, A. (2013). Selection of habitat by the jaguar, *Panthera onca* (Carnivora: Felidae), in the upper Paraná River, Brazil. *Zool. Curitiba* *30*, 379–387.
66. Kareiva, P., and Odell, G. (1987). Swarms of predators exhibit "preyaxis" if individual predators use area-restricted search. *Am. Nat.* *130*, 233–270.
67. Fahrig, L. (2007). Non-optimal animal movement in human-altered landscapes. *Funct. Ecol.* *21*, 1003–1015.
68. Dickson, B.G., Jenness, J.S., and Beier, P. (2005). Influence of vegetation, topography, and roads on cougar movement in Southern California. *J. Wildl. Manage.* *69*, 264–276.
69. Oriol-Cotterill, A., Macdonald, D.W., Valeix, M., Ekwanga, S., and Frank, L.G. (2015). Spatiotemporal patterns of lion space use in a human-dominated landscape. *Anim. Behav.* *101*, 27–39.
70. Valeix, M., Hemson, G., Loveridge, A.J., Mills, G., and Macdonald, D.W. (2012). Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape: wild prey, livestock and lion ecology. *J. Appl. Ecol.* *49*, 73–81.
71. Valeix, M., Loveridge, A.J., Davidson, Z., Madzikanda, H., Fritz, H., and Macdonald, D.W. (2010). How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landsc. Ecol.* *25*, 337–351.
72. Wilmers, C.C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M.L., Kermish-Wells, J., Yovovich, V., and Williams, T. (2013). Scale dependent behavioral responses to human development by a large predator, the puma. *PLoS ONE* *8*, e60590.
73. Petracca, L.S., Frair, J.L., Bastille-Rousseau, G., Hunt, J.E., Macdonald, D.W., Sibanda, L., and Loveridge, A.J. (2019). The effectiveness of hazing African lions as a conflict mitigation tool: implications for carnivore management. *Ecosphere* *10*, 14.
74. Nickel, B.A., Suraci, J.P., Nisi, A.C., and Wilmers, C.C. (2021). Energetics and fear of humans constrain the spatial ecology of pumas. *Proc. Natl. Acad. Sci. USA* *118*, e2004592118.
75. Suraci, J.P., Clinchy, M., Zanette, L.Y., and Wilmers, C.C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecol. Lett.* *22*, 1578–1586.
76. Noonan, M.J., Fleming, C.H., Akre, T.S., Drescher-Lehman, J., Gurarie, E., Harrison, A.-L., Kays, R., and Calabrese, J.M. (2019). Scale-insensitive estimation of speed and distance traveled from animal tracking data. *Mov. Ecol.* *7*, 35.
77. Simcharoen, A., Savini, T., Gale, G.A., Simcharoen, S., Duangchantrasiri, S., Pakpien, S., and Smith, J.L.D. (2014). Female tiger *Panthera tigris* home range size and prey abundance: important metrics for management. *Oryx* *48*, 370–377.
78. Loveridge, A.J., Valeix, M., Elliot, N.B., and Macdonald, D.W. (2017). The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. *J. Appl. Ecol.* *54*, 815–825.
79. Suraci, J.P., Frank, L.G., Oriol-Cotterill, A., Ekwanga, S., Williams, T.M., and Wilmers, C.C. (2019). Behavior-specific habitat selection by African lions may promote their persistence in a human-dominated landscape. *Ecology* *100*, e02644.
80. Odden, M., Athreya, V., Rattan, S., and Linnell, J.D.C. (2014). Adaptable neighbours: movement patterns of GPS-collared leopards in human dominated landscapes in India. *PLoS ONE* *9*, e112044.
81. Athreya, V., Odden, M., Linnell, J.D.C., Krishnaswamy, J., and Karanth, K.U. (2016). A cat among the dogs: leopard *Panthera pardus* diet in a human-dominated landscape in western Maharashtra, India. *Oryx* *50*, 156–162.
82. Jacobson, A.P., Gerngross, P., Lemeris, J.R., Jr., Schoonover, R.F., Anco, C., Breitenmoser-Würsten, C., Durant, S.M., Farhadinia, M.S., Henschel, P., Kamler, J.F., et al. (2016). Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. *PeerJ* *4*, e1974.
83. Sunquist, M.E., and Sunquist, F.C. (2002). *Wild Cats of the World* (University of Chicago Press).
84. Hayward, M.W., Kamler, J.F., Montgomery, R.A., Newlove, A., Rostro-García, S., Sales, L.P., and Van Valkenburgh, B. (2016). Prey preferences of the jaguar *Panthera onca* reflect the post-Pleistocene demise of large prey. *Front. Ecol. Evol.* *3*, 148.
85. Thompson, J.J., Martí, C.M., and Quigley, H. (2020). Anthropogenic factors disproportionately affect the occurrence and potential population connectivity of the Neotropic's apex predator: the jaguar at the south-western extent of its distribution. *Glob. Ecol. Conserv.* *24*, 01356.
86. Romero-Muñoz, A., Torres, R., Noss, A.J., Giordano, A.J., Quiroga, V., Thompson, J.J., Baumann, M., Altrichter, M., McBride, R., Velilla, M., et al. (2019). Habitat loss and overhunting synergistically drive the extirpation of jaguars from the Gran Chaco. *Divers. Distrib.* *25*, 176–190.
87. McBride, R.T., and Thompson, J.J. (2019). Spatial ecology of Paraguay's last remaining Atlantic forest Jaguars (*Panthera onca*): implications for their long-term survival. *Biodiversity (Nepean)* *20*, 20–26.

88. González-Gallina, A., Hidalgo-Mihart, M.G., Pérez-Garduza, F., Iglesias-Hernández, J.A., Oliveras de Ita, A., Chacón-Hernández, A., and Vázquez-Zúñiga, O. (2017). Home range of a male jaguar spatially associated with the landfill of the city of Playa del Carmen, Mexico. *Mammalia* 82, 54–61.
89. Kays, R., Crofoot, M.C., Jetz, W., and Wikelski, M. (2015). ECOLOGY. Terrestrial animal tracking as an eye on life and planet. *Science* 348, aaa2478.
90. Macdonald, D.W. (2016). Animal behaviour and its role in carnivore conservation: examples of seven deadly threats. *Anim. Behav.* 120, 197–209.
91. Van Moorter, B., Rolandsen, C.M., Basille, M., and Gaillard, J.-M. (2016). Movement is the glue connecting home ranges and habitat selection. *J. Anim. Ecol.* 85, 21–31.
92. Convention on the Conservation of Migratory Species of Wild Animals (2020). *Panthera onca*. <https://www.cms.int/en/species/panthera-onca>.
93. GSLEP (2019). Global Snow Leopard and Ecosystem Protection Program. <https://www.globalsnowleopard.org/>.
94. World Bank (2011). Global tiger recovery program (2010-2022) (World Bank).
95. Carter, N., Killion, A., Easter, T., Brandt, J., and Ford, A. (2020). Road development in Asia: assessing the range-wide risks to tigers. *Sci. Adv.* 6, z9619.
96. Henschel, P., Coad, L., Burton, C., Chataigner, B., Dunn, A., MacDonald, D., Saidu, Y., and Hunter, L.T.B. (2014). The lion in West Africa is critically endangered. *PLoS ONE* 9, e83500.
97. Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L.T.B., Macdonald, D.W., and Packer, C. (2015). Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proc. Natl. Acad. Sci. USA* 112, 14894–14899.
98. Morato, R.G., Thompson, J.J., Paviolo, A., de La Torre, J.A., Lima, F., McBride, R.T., Jr., Paula, R.C., Cullen, L., Jr., Silveira, L., Kantek, D.L.Z., et al. (2018). Jaguar movement database: a GPS-based movement dataset of an apex predator in the Neotropics. *Ecology* 99, 1691.
99. Calabrese, J.M., Fleming, C.H., and Gurarie, E. (2016). ctm: an R package for analyzing animal relocation data as a continuous-time stochastic process. *Methods Ecol. Evol.* 7, 1124–1132.
100. R Development Core Team (2019). R: a language and environment for statistical computing (R Foundation for Statistical Computing).
101. Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48.
102. Lunn, D.J., Thomas, A., Best, N., and Spiegelhalter, D. (2000). WinBUGS - a Bayesian modelling framework: concepts, structure, and extensibility. *Stat. Comput.* 10, 325–337.
103. Sturtz, S., Ligges, U., and Gelman, A. (2005). R2WinBUGS: a package for running WinBUGS from R. *J. Stat. Softw.* 12, 1–16.
104. Barton, K. (2009). MUMIn: multi-model inference (R Package Version 0.12.2/r18). <http://R-Forge.R-project.org/projects/mumin/>.
105. Makowski, D., Ben-Shachar, M., and Lüdtke, D. (2019). bayestestR: describing effects and their uncertainty, existence and significance within the Bayesian framework. *J. Open Source Softw.* 4, 1541.
106. Wickham, H. (2016). ggplot2: elegant graphics for data analysis (Springer-Verlag).
107. 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.
108. IUCN and UNEP-WCMC (2018). The World Database on Protected Areas (WDPA). www.protectedplanet.net.
109. Fick, S.E., and Hijmans, R.J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37, 4302–4315.
110. Zhao, M., Heinsch, F.A., Nemani, R.R., and Running, S.W. (2005). Improvements of the MODROS. Inf. Serv. terrestrial gross and net primary production global data set. *Remote Sens. Environ.* 95, 164–176.
111. CIESIN (2018). Gridded Population of the World, Version 4 (GPW), v4: Population Density, Revision 11. <https://sedac.ciesin.columbia.edu/data/set/gpw-v4-population-density-rev11>.
112. 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.
113. Robinson, T.P., Wint, G.R.W., Conchedda, G., Van Boeckel, T.P., Ercoli, V., Palamara, E., Cinardi, G., D'Aiuti, L., Hay, S.I., and Gilbert, M. (2014). Mapping the global distribution of livestock. *PLoS ONE* 9, e96084.
114. CIESIN and ITOS (2013). Global Roads Open Access Data Set, Version 1 (gROADS), v1. <https://sedac.ciesin.columbia.edu/data/set/groads-global-roads-open-access-v1>.
115. Sikes, R.S.; Animal Care and Use Committee of the American Society of Mammalogists (2016). 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *J. Mammal.* 97, 663–688.
116. Fleming, C.H., Fagan, W.F., Mueller, T., Olson, K.A., Leimgruber, P., and Calabrese, J.M. (2015). Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology* 96, 1182–1188.
117. Noonan, M.J., Tucker, M.A., Fleming, C.H., Akre, T.S., Alberts, S.C., Ali, A.H., Altmann, J., Antunes, P.C., Belant, J.L., Beyer, D., et al. (2019). A comprehensive analysis of autocorrelation and bias in home range estimation. *Ecol. Monogr.* 89, e01344.
118. Fleming, C.H., and Calabrese, J.M. (2017). A new kernel density estimator for accurate home-range and species-range area estimation. *Methods Ecol. Evol.* 8, 571–579.
119. Burt, W.H. (1943). Territoriality and home range concepts as applied to mammals. *J. Mammal.* 24, 346.
120. Kéry, M., and Schaub, M. (2012). Bayesian Population Analysis Using WinBUGS: A Hierarchical Perspective, First Edition (Academic Press).
121. Burnham, K.P., and Anderson, D.R. (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (Springer).
122. Arnold, T.W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *J. Wildl. Manage.* 74, 1175–1178.
123. Fleming, C.H., Noonan, M.J., Medici, E.P., and Calabrese, J.M. (2019). Overcoming the challenge of small effective sample sizes in home-range estimation. *Methods Ecol. Evol.* 10, 1679–1689.
124. Worton, B.J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70, 164–168.
125. Fleming, C.H., Sheldon, D., Fagan, W.F., Leimgruber, P., Mueller, T., Nandintsetseg, D., Noonan, M.J., Olson, K.A., Setyawan, E., Sianipar, A., and Calabrese, J.M. (2018). Correcting for missing and irregular data in home-range estimation. *Ecol. Appl.* 28, 1003–1010.
126. Kéry, M. (2010). Introduction to WinBUGS for Ecologists: A Bayesian Approach to Regression, ANOVA, Mixed Models and Related Analyses, First Edition (Elsevier).
127. Schielzeth, H., and Forstmeier, W. (2009). Conclusions beyond support: overconfident estimates in mixed models. *Behav. Ecol.* 20, 416–420.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental models: Organisms/strains		
<i>Panthera onca</i>	Wild	N/A
Deposited Data		
Raw data	98	https://doi.org/10.5061/dryad.2dh0223
Software and algorithms		
<i>ctmm</i> 0.5.11	99	https://cran.r-project.org/web/packages/ctmm/index.html
R 3.6.3	100	https://www.r-project.org/
<i>lme4</i> 1.1-23	101	https://cran.r-project.org/web/packages/lme4/index.html
<i>WinBUGS</i> 1.4.3	102	https://www.mrc-bsu.cam.ac.uk/software/bugs/the-bugs-project-winbugs/
<i>R2WinBUGS</i> 2.1-21	103	https://cran.r-project.org/web/packages/R2WinBUGS/index.html
<i>MuMIn</i>	104	https://cran.r-project.org/web/packages/MuMIn/index.html
<i>bayestestR</i>	105	https://cran.r-project.org/web/packages/bayestestR/index.html
<i>ggplot2</i>	106	https://ggplot2.tidyverse.org
Other		
Terrestrial ecoregions	13	https://ecoregions2017.appspot.com/
Forest cover	107	https://www.globalforestwatch.org/
Protected area	108	https://www.protectedplanet.net/
Annual precipitation	109	http://worldclim.org/
Seasonality in precipitation	109	http://worldclim.org/
Net primary productivity	110	http://files.ntsg.umd.edu/data/NTSG_Products/MOD17/
Human pop density	111	https://sedac.ciesin.columbia.edu/data/set/gpw-v4-population-density-rev11
Human footprint index	112	https://wchumanfootprint.org/
Cattle density	113	https://livestock.geo-wiki.org/home-2/
Primary Roads	114	https://sedac.ciesin.columbia.edu/data/set/groads-global-roads-open-access-v1

RESOURCE AVAILABILITY

Lead Contact

Further information and requests should be directed to and will be fulfilled by the Lead Contact, Jeffrey J. Thompson (jthompson.py@gmail.com).

Materials Availability

This study did not generate unique reagents.

Data and Code Availability

- Original telemetry data are deposited to Data Dryad: <https://doi.org/10.5061/dryad.2dh0223>.
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Ethics statement

The study subjects were jaguars *Panthera onca*. All jaguar captures and handling were undertaken with permission of their respective range state and followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research.¹¹⁵

METHOD DETAILS

Telemetry data

Our dataset was comprised of published GPS telemetry data from 106 jaguars (49 males, 57 females),⁹⁸ and additional data from 2 jaguars (1 male, 1 female) from the Colombian Llanos and 3 males from the Southwestern Amazon moist forests in Peru. We developed 115 telemetry trajectories for 111 jaguars from 24 sites in 7 countries and 13 ecoregions (Figure 4). The data from four individuals were separated into two distinct sampling periods each as they were monitored for two periods that were separated by two to three years. Our data were representative of tropical and subtropical grasslands, savannas, shrublands, moist and dry broadleaf forests, and flooded grassland and savanna which, with the exception of mangrove forest, constitute all the biomes inhabited by jaguars.^{9,13}

Covariates

Based upon previous research on factors related to jaguar distribution and home range size, as well as other carnivores,^{10–12,29,32,33,50,67,87} we hypothesized that nine environmental and four anthropogenic covariates could potentially be determinants of home range size of jaguar across its distribution. For each home range area, we derived the 1) mean percent forest cover,¹⁰⁷ 2) mean percent area in forest,¹⁰⁷ 3) mean forest patch area,¹⁰⁷ 4) perimeter:area ratio of forest patches,¹⁰⁷ 5) density of forest edge,¹⁰⁷ 6) percent protected area,¹⁰⁸ 7) mean annual precipitation,¹⁰⁹ 8) mean seasonality in precipitation,¹⁰⁹ 9) mean net primary productivity,¹¹⁰ 10) mean human population density,¹¹¹ 11) mean Human Footprint Index,¹¹² 12) mean cattle density,¹¹³ and 13) primary road density.¹¹⁴ If available, covariates were derived from data that corresponded to the year when the majority of telemetry locations for each individual were obtained, otherwise we used the dataset that was most close in time to when the telemetry data were collected. Additionally, we included sex as a covariate based upon exploratory analysis of the data and that sex-based differences in jaguar movements have been illustrated,^{29,30,50,64} while we also considered the effect of body mass as it has been shown to be a factor associated with jaguar distribution.¹⁰

We tested for correlation among covariates using Pearson's Correlation Coefficient, with coefficient values between -0.6 – 0.6 considered uncorrelated. Of the original covariate set, seven were uncorrelated with other covariates; mean percent forest cover, percent protected area, mean annual precipitation, mean seasonality in precipitation, mean net primary productivity, mean human population density, and road density (Table S6). Also, body mass was significantly associated with sex (Kruskal-Wallis χ^2 test, $p = 0.04$) and was not included in the models. We expected that home range size and speed would decrease, and tortuosity increase (measured as velocity autocorrelation timescale), in relation to increasing habitat quality measured as increasing forest cover, percent protected area, mean annual precipitation, and mean net primary productivity. Concurrently, mean seasonality in precipitation, mean human population density, and road density were expected to directly or indirectly reduce habitat quality for jaguars which were expected to be positively associated with home range size and speed and inversely related with tortuosity.^{10,12,29,32,50,67,87,98}

QUANTIFICATION AND STATISTICAL ANALYSIS

Workflow

For our analysis we developed a multi-step workflow (Figure S2; see details below) to estimate home range size and movement parameters, controlling for the reliability of estimates based upon effective sample size. Since not accounting for autocorrelation inherent in GPS telemetry data when characterizing animal movements can produce biased home range and speed estimates,^{76,116,117} we fit continuous-time stochastic process (CTSP) models to our data to estimate home range area and speed as these models account for spatial autocorrelation by separating the discrete-time sampling process of telemetry from the continuous-time movement process.

For each individual we first determined range-residency by examining variograms of semi-variance versus time lags for each telemetry trajectory. Individuals were considered range resident when semi-variance increased and then stabilized with increasing time lags.^{14,99} For individuals demonstrating range residency we estimated home ranges with area-corrected autocorrelated kernel density estimation (AKDEc),^{99,116,118} while individuals that did not demonstrate range-residency were excluded from further analysis. We note that in estimating home range size we employed the definition of Burt,¹¹⁹ defining a home range as “that area traversed by the individual in its normal activities of food gathering, mating, and caring for young.” Furthermore, as the typically used measure of speed is based upon the straight-line distance between two consecutive points over time is sensitive to sampling scale and biased due to the effects of path tortuosity, sampling frequency, and location error, we employed continuous-time speed estimation⁷⁶ to overcome these biases.

We examined the relationship of estimates of home range size, speed, and velocity autocorrelation timescale (tortuosity) to landscape-level environmental and anthropogenic covariates using generalized linear mixed models (GLMM)¹²⁰ in a maximum likelihood framework with ecoregion as a random intercept, ranking models using Akaike Information Criteria adjusted for small sample size (AICc).¹²¹ Using informative parameters from top ranking model sets,¹²² we then estimated parameter effects within a Bayesian framework which facilitated estimating the effect size of parameters and quantifying the probabilities of covariate effects based upon posterior distributions.¹²⁰

Home range and movement parameter estimation

After determining range residency for individuals, we fit CTSP models to the telemetry data using perturbative hybrid residual maximum likelihood with starting values derived from semi-variance functions, and ranking model fit using *AICc*.^{14,99,118,123} We undertook the estimation of home range and movement parameters with the *ctmm* package⁹⁹ in R,¹⁰⁰ which considers a suite of potential movement models which included 1) an independent identically distributed (IID) process which assumes a lack of correlation in positions and velocities which is the assumption of traditional kernel density home range estimation,¹²⁴ 2) a random search model with constrained space use to a finite home range Ornstein–Uhlenbeck, OU, 3) the Ornstein–Uhlenbeck motion model with foraging OUF which is the OU process with correlated velocities allowing for the estimation of the velocity autocorrelation timescale time over which movements are correlated and mean distance traveled per day (Gaussian estimates of the root mean speed), 4) a special case of the OUF model (OUf) where the velocity autocorrelation timescale and the position autocorrelation timescale are equal, and 5) the $OU\Omega$ model which is the OUf model with oscillatory range crossing.^{14,99}

We used the best fit CTSP model to estimate optimally weighted 95% AKDEc home ranges^{116,118,123,125} while estimates of velocity autocorrelation timescale were generated when the OUF or OUf models best described the data. Where the effective sample size, as measured by the number of home range crossings during the sample period, was less than 3.5 we excluded those individuals from the analysis as model estimates were unreliable, while for individuals where the effective sample size was 3.5–5 we used parametric bootstrapping to reduce bias in the model estimates.¹²³

Although for individuals where the OUF or OUf model were the best movement model Gaussian estimates of the root mean speed are generated, these estimates are not always proportional to the total distance traveled, nor are velocities always normally distributed as assumed by a Gaussian process.⁷⁶ Consequently we followed the workflow of⁷⁶ to estimate non-Gaussian speed⁹⁹ to account for irregular sampling and to incorporate location error into model fit. When effective sample size for velocity estimation was low, caused when the sampling interval was greater than three times the velocity autocorrelation timescale, information to reliably estimate speed was insufficient and consequently we excluded those estimates from the analysis.⁷⁶ If estimates of location error were not available for an individual, we used a value of 10 m which was consistent with available error estimates and, given the scale of jaguar movements in relation to GPS error, we found that speed estimates were insensitive to increases in error values. Consequently, we were confident that our choice in an error value did not introduce any notable bias into our speed estimates.¹²⁵

Semi-variogram analysis, model selection, weighted AKDEc, parametric bootstrapping, and speed estimation were undertaken using the *ctmm* package⁹⁹ with the software R.¹⁰⁰ Irregular sampling schedules in the data were accounted for using the *dt* argument within the *variogram* function in the *ctmm* package.⁹⁹

Model selection and specification

We modeled the relationship of the estimates of home range, speed, and velocity autocorrelation timescale with the covariates using generalized linear mixed models (GLMM)¹²⁰ in maximum likelihood and Bayesian frameworks. We chose to employ GLMMs, with ecoregion as a random intercept, since it allowed for our inferences to be extrapolated to the entire jaguar population since our data by ecoregion are considered samples from the entire jaguar population.^{120,126} Also, the random effect allowed for borrowing of information and improved accounting of unstructured variability of individuals within groups, uncertainty stemming from small sample sizes in some ecoregions, and potential pseudoreplication in our data stemming from intra-level correlations or lack of independence when more than one individual was tracked at the same place and time.^{120,126} We note that we attempted to include slope as a random effect to better control for error in our estimates¹²⁷ but models were singular or failed to converge due to our sample size.

We first modeled covariate relationships with home range size, speed, and velocity autocorrelation timescale in a maximum likelihood framework to undertake model selection and identify informative parameters based upon *AICc* and to minimize computational time. Dependent variables (home range size, speed and velocity autocorrelation timescale estimates) were log-transformed to ensure normality, as determined with Shapiro-Wilk tests and inspection of Q-Q plots, and to facilitate model convergence. Similarly, to aid in model convergence, covariates were log transformed or z-transformed so that their mean values were equal to zero.

Given concerns of over-parameterizing and over-fitting a global model directly in a Bayesian framework we first used *AIC*-based model selection in a maximum-likelihood framework to identify a most parsimonious model or model set, ensuring that all parameters were informative at a 85% significance level¹²² (Tables S2 and S3) which justifies inclusion of the parameter in a model as *AIC* has a tendency to favor more complex models which include uninformative parameters.^{121,122} We tested the relationship of all combinations of the covariates with home range size, speed, and velocity autocorrelation timescale using ecoregion as a random intercept, selecting top ranking model set as all models within two *AICc* values of the top ranking models.¹²¹

We then selected all parameters from the top-ranking model sets for home range size and movement parameters to be included in models to be evaluated in a Bayesian framework. By including the covariates included in the top ranking model set in a single model in a Bayesian framework allowed us to easily estimate the effect size of parameters and probability of an effect from covariates based upon posterior distributions.¹²⁰ Although we could have directly evaluated the global model in a Bayesian framework, taking the position that parameter effects would be fractional based upon the data and model,¹²⁰ we were concerned with over-fitting and over-parameterization of a model with eight covariates and consequently, we used a hybrid approach to identify the most informative parameters to be included in our final models.

For modeling maximum likelihood GLMMs we used the *lme4* package¹⁰¹ with the software R¹⁰⁰ and conducted multi-model selection using the *MuMIn* package.¹⁰⁴ For running the Bayesian GLMMs we used *WinBUGS*¹⁰² and the *R2winBUGS* package,¹⁰³ running 3 chains for 1 million iterations, a burn-in period of 100,000 iterations, and a thinning rate of 30. For the prior distributions

in the modeling we used diffuse uniform distributions for the random effects and normal distributions for the covariate effects, confirming model convergence with a scale reduction factor <1.01 and visual inspection of trace plots.

The probability of a covariate effect on home range size and movement parameters from the Bayesian GLMM was measured by the proportion of the parameter posterior distributions above or below 0 (no effect) and we tested for differences in home range and movement parameters between sexes and among ecoregions using the proportional overlap of posterior distributions. Analyses of posterior distributions were undertaken using the `bayestestR` package.¹⁰⁵

Using the parameter estimates for each covariate for each ecoregion and the spatial covariate values we predicted mean home range size for the portion of each study ecoregion that overlapped with the jaguar's distribution,⁹ and using the ecoregion hyperparameter as the mean value of the intercept, predicted relative home range size across the jaguars distribution. We tested the relationship between our estimated mean home size per ecoregion with density estimates from the literature for each ecoregion^{17–28} using a Pearson's Correlation Coefficient. All spatial data and maps were at a resolution of 0.008 decimal degrees (approximately 1 km).