

Factors influencing terrestriality in primates of the Americas and Madagascar

Eppley, Timothy M.; Hoeks, Selwyn; Chapman, Colin A.; Ganzhorn, Jörg U. ; Hall, Katie; Owen, Megan A.; Adams, Dara B.; Allgas, Néstor ; Amato, Katherine R. ; Andriamahaiavana, McAntonin ; Aristizabal, John F. ; Baden, Andrea L. ; Balestri, Michela ; Barnett, Adrian; Bicca-Marques, Julio Cesar; Bowler, Mark; Boyle, Sarah A.; Brown, Meredith ; Caillaud, Damien ; Calegario-Marques, Cláudia ; Campbell, Christina J. ; Campera, Marco ; Campos, Fernando A. ; Cardoso, Tatiane S. ; Carretero-Pinzón, Xyomara ; Champion, Jane ; Chaves, Óscar M. ; Chen-Kraus, Chloe ; Colquhoun, Ian C. ; Dean, Brittany ; Dubrueil, Colin ; Ellis, Kelsey M. ; Erhart, Elizabeth M. ; Evans, Kayley J. E. ; Fedigan, Linda M. ; Felton, Annika; Ferreira, Renata G. ; Fichtel, Claudia ; Fonseca, Manuel L. ; Fontes, Isadora P. ; Fortes, Vanessa B. ; Fumian, Ivanyr ; Gibson, Dean; Guzzo, Guilherme B. ; Hartwell, Kayla S.; Heymann, Eckhard W. ; Hilário, Renato R. ; Holmes, Sheila M. ; Irwin, Mitchell T.; Johnson, Steig E. ; Kappeler, Peter M. ; Kelley, Elizabeth A. ; King, Tony; Knogge, Christoph ; Koch, Flávia; Kowalewski, Martin M. ; Lange, Liselot R. ; Lauterbur, M. Elise ; Louis, Jr, Edward E. ; Lutz, Meredith C. ; Martínez, Jesús ; Melin, Amanda D. ; de Melo, Fabiano R. ; Mihaminekena, Tsimisento H. ; Mogilewsky, Monica S. ; Moreira, Leandro S. ; Moura, Letícia A. ; Muhle, Carina B. ; Nagy-Reis, Mariana B. ; Norconk, Marilyn A. ; Notman, Hugh ; O'Mara, M. Teague ; Ostner, Julia ; Patel, Erik R. ; Pavelka, Mary S. M. ; Pinacho-Guendulain, Braulio ; Porter, Leila M. ; Pozo-Montuy, Gilberto ; Raboy, Becky E. ; Rahalinarivo, Vololonirina ; Raharinoro, Njaratiana A. ; Rakotomalala, Zafimahery ; Ramos-Fernández, Gabriel; Rasamisoa, Delaïd C. ; Ratsimbazafy, Jonah; Ravaloharimanitra, Maholy ; Ravaloharimanitra, Josia; Razanaparany, Tojotanjona P. ; Righini, Nicoletta ; Robson, Nicola M. ; da Rosa Gonçalves, Jonas ; Sanamo, Justin; Santacruz, Nicole ; Sato, Hiroki; Sauther, Michelle L. ; Scarry, Clara J. ; Carlos Serio-Silva, Juan; Shanee, Sam; de Souza Lins, Poliana G. A. ; Smith, Andrew C.; Smith Aguilar, Sandra E. ; Souza-Alves, João Pedro ; Stavis, Vanessa Katherinne ; Steffens, Kim J. E.; Stone, Anita I. ; Strier, Karen B. ; Stier, Karen B. ; Talebi, Maurício; Tecot, Stacey R.; Tujague, M. Paula ; Tujague, Kim; Van Belle, Sarie ; Vasey, Natalie; Wallace, Robert B. ; Welch, Gilroy ; Wright, Patricia C. ; Donati, Guiseppe; Santini, Luca

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Main Manuscript for

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Timothy M. Eppley^{a,b,1}, Selwyn Hoeks^c, Colin A. Chapman^{d,e,f,g}, Jörg U. Ganzhorn^h, Katie Hallⁱ, Megan A. Owen^a, Dara B. Adams^{j,k}, Néstor Allgas^l, Katherine R. Amato^m, McAntonin Andriamahaiavanaⁿ, John F. Aristizabal^{o,p}, Andrea L. Baden^{q,r,s}, Michela Balestri^t, Adrian A. Barnett^{u,v}, Júlio César Bicca-Marques^w, Mark Bowler^{a,x,y}, Sarah A. Boyle^z, Meredith Brown^{aa}, Damien Caillaud^{bb}, Cláudia Calegari-Marques^{cc}, Christina J. Campbell^{dd}, Marco Campera^t, Fernando A. Campos^{ee}, Tatiane S. Cardoso^{ff}, Xyomara Carretero-Pinzón^{gg}, Jane Champion^{aa}, Óscar M. Chaves^{hh}, Chloe Chen-Krausⁱⁱ, Ian C. Colquhoun^{jj}, Brittany Dean^{aa}, Colin Dubrueil^{aa}, Kelsey M. Ellis^{kk}, Elizabeth M. Erhart^{ll}, Kayley J. E. Evans^{aa}, Linda M. Fedigan^{aa}, Annika M. Felton^{mmm}, Renata G. Ferreiraⁿⁿ, Claudia Fichtel^{oo}, Manuel L. Fonseca^{pp}, Isadora P. Fontes^{qq,rr}, Vanessa B. Fortes^{ss}, Ivanyr Fumian^{tt}, Dean Gibson^a, Guilherme B. Guzzo^{uu}, Kayla S. Hartwell^{aa,vv}, Eckhard W. Heymann^{oo}, Renato R. Hilário^{ww}, Sheila M. Holmes^{xx}, Mitchell T. Irwin^{yy}, Steig E. Johnson^{aa}, Peter M. Kappeler^{oo,zz}, Elizabeth A. Kelley^{ab}, Tony King^{ac,ad,ae}, Christoph Knogge^{af}, Flávia Koch^{oo}, Martin M. Kowalewski^{ag}, Liselot R. Lange^{ah,ai}, M. Elise Lauterbur^{aj,ak}, Edward E. Louis, Jr.^{al}, Meredith C. Lutz^{am}, Jesús Martínez^{an,ao}, Amanda D. Melin^{aa}, Fabiano R. de Melo^{ap,aq}, Tsimisento H. Mihaminekena^{ac,ar}, Monica S. Mogilewsky^{as}, Leandro S. Moreira^{tt,aq}, Letícia A. Moura^{aq,at}, Carina B. Muhle^w, Mariana B. Nagy-Reis^{au}, Marilyn A. Norconk^{av}, Hugh Notman^{aa,aw}, M. Teague O'Mara^{ax,ay,az}, Julia Ostner^{ba,bc}, Erik R. Patel^{bd}, Mary S. M. Pavelka^{aa}, Braulio Pinacho-Guendulain^{be,bf}, Leila M. Porter^{yy}, Gilberto Pozo-Montuy^{bg,cw}, Becky E. Raboy^{bh}, Vololonirina Rahalinarivo^{bi}, Njaratiana A. Raharinoroⁿ, Zafimahery Rakotomalalaⁿ, Gabriel Ramos-Fernández^{bj,bk}, Delaïd C. Rasamisoa^a, Jonah

25 Ratsimbazafy ^{ar}, Maholy Ravaloharimanitra ^{ac}, Josia Razafindramanana ^{bi}, Tojotanjona P.
26 Razanaparany ^{bl,n}, Nicoletta Righini ^{bm}, Nicola M. Robson ^{bn}, Jonas da Rosa Gonçalves ^{bp}, Justin
27 Sanamo ^{bq}, Nicole Santacruz ^{br}, Hiroki Sato ^{bs}, Michelle L. Sauther ^{bt}, Clara J. Scarry ^{bu,bv}, Juan
28 Carlos Serio-Silva ^{bw}, Sam Shanee ^{bx}, Poliana G. A. de Souza Lins ^{by}, Andrew C. Smith ^{bz},
29 Sandra E. Smith Aguilar ^{ca}, João Pedro Souza-Alves ^{cb,cd}, Vanessa Katherinne Stavis ^{ce,cf}, Kim J.
30 E. Steffens ^{cg}, Anita I. Stone ^{ch}, Karen B. Strier ^{ci}, Scott A. Suarez ^{cj}, Maurício Talebi ^{ck,cl}, Stacey
31 R. Tecot ^{cm}, M. Paula Tujague ^{cn,co,cp}, Kim Valenta ^{cq}, Sarie Van Belle ^{cr}, Natalie Vasey ^{b,vv},
32 Robert B. Wallace ^{an,cs,ao}, Gilroy Welch ^{vv}, Patricia C. Wright ^{ct,cu}, Giuseppe Donati ^{t,2}, Luca
33 Santini ^{cv,2}

34
35 ^a Conservation Science and Wildlife Health, San Diego Zoo Wildlife Alliance, Escondido, CA
36 92027

37 ^b Department of Anthropology, Portland State University, Portland, OR 97201

38 ^c Department of Environmental Science, Radboud Institute for Biological and Environmental
39 Sciences (RIBES), Radboud University, 6500 GL Nijmegen, The Netherlands

40 ^d Department of Anthropology, Center for the Advanced Study of Human Paleobiology, The
41 George Washington University, Washington D.C. 20037

42 ^e Wilson Center, 1300 Pennsylvania Avenue NW, Washington, D.C. 20004

43 ^f School of Life Sciences, University of KwaZulu-Natal, Scottsville, Pietermaritzburg, South
44 Africa

45 ^g Shaanxi Key Laboratory for Animal Conservation, Northwest University, Xi'an 710069, China

46 ^h Department of Animal Ecology and Conservation, Institute of Zoology, Universität Hamburg,
47 20146 Hamburg, Germany

48 ⁱ Sedgwick County Zoo, Wichita, KS 67212

49 ^j Department of Anthropology, The Ohio State University, Columbus, OH 43210

50 ^k Department of Anthropology, Humboldt State University, Arcata, CA 95521

51 ^l Asociación Neotropical Primate Conservation Perú, Moyobamba, San Martin, Perú

52 ^m Department of Anthropology, Northwestern University, Evanston 60208

53 ⁿ Mention Zoologie et Biodiversité Animale, Faculté des Sciences, Université d'Antananarivo,
54 101 Antananarivo, Madagascar

55 ^o Departamento de Ciencias Químico Biológicas, Instituto de Ciencias Biomédicas, Universidad
56 Autónoma de Ciudad Juárez, Ciudad Juárez, México

57 ^p Laboratorio de Ecología de Bosques Tropicales y Primatología, Departamento de Ciencias
58 Biológicas, Universidad de Los Andes, Bogotá, 111711, Colombia

59 ^q Department of Anthropology, Hunter College of City University of New York, NY 10065

60 ^r Department of Anthropology, The Graduate Center of City University of New York, NY 10016

61 ^s The New York Consortium in Evolutionary Primatology (NYCEP), New York, NY

62 ^t Department of Social Sciences, Oxford Brookes University, Oxford OX3 0BP, UK

63 ^u Centre for Research in Evolutionary and Environmental Anthropology, Roehampton
64 University, London SW15 5PJ, UK

65 ^v Department of Zoology, Federal University of Pernambuco, Recife-PE, 50670-901, Brazil

66 ^w Laboratório de Primatologia, Escola de Ciências da Saúde e da Vida, Pontifícia Universidade
67 Católica do Rio Grande do Sul, PUCRS, Porto Alegre-RS, 90619-900, Brazil

68 ^x Department of Engineering, Arts, Science and Technology, University of Suffolk, Ipswich IP4
69 1QJ, UK

70 ^y Suffolk Sustainability Institute, Ipswich IP4 1QJ, UK

71 ^z Department of Biology, Rhodes College, Memphis, TN 38112

72 ^{aa} Department of Anthropology & Archaeology, University of Calgary, Calgary, Alberta, T2N
73 1N4, Canada

74 ^{bb} Department of Anthropology, University of California, Davis, CA, 95616

75 ^{cc} Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre-RS,
76 90650-001, Brazil.

77 ^{dd} Department of Anthropology, California State University Northridge, Northridge, CA 91325

78 ^{ee} Department of Anthropology, University of Texas at San Antonio, San Antonio, TX 78249

79 ^{ff} Coordenação de Ciências da Terra e Ecologia, Museu Paraense Emílio Goeldi, Belém-PA,
80 66077-830, Brazil

81 ^{gg} Proyecto Zocay, Colombia

82 ^{hh} Escuela de Biología, Universidad de Costa Rica, San José, 11501-2060, Costa Rica

83 ⁱⁱ Department of Anthropology, Yale University, New Haven, CT 06511

84 ^{jj} Department of Anthropology and The Centre for Environment & Sustainability, University of
85 Western Ontario, London, Ontario, N6A 3K7, Canada
86 ^{kk} Department of Anthropology, Miami University, Oxford, OH 45056
87 ^{ll} Department of Anthropology, Texas State University, San Marcos, TX 78666
88 ^{mmm} Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences
89 (SLU), Alnarp, Sweden
90 ⁿⁿ Pós-Graduação em Psicobiologia, Universidade Federal do Rio Grande do Norte, Natal-RN,
91 59078-970, Brazil
92 ^{oo} Behavioral Ecology and Sociobiology Unit, German Primate Center, 37077 Göttingen,
93 Germany
94 ^{pp} Laboratorio de Ecología de Bosques Tropicales y Primatología, Departamento de Ciencias
95 Biológicas, Universidad de los Andes, Bogotá, 111711, Colombia
96 ^{qq} Programa de Pós-graduação em Desenvolvimento e Meio Ambiente, Universidade Federal de
97 Sergipe, São Cristóvão-SE, 49100-000, Brazil
98 ^{rr} Secretaria Municipal de Meio Ambiente, Aracaju-SE, 49015-190, Brazil
99 ^{ss} Laboratório de Primatologia, Departamento de Zootecnia e Ciências Biológicas, Universidade
100 Federal de Santa Maria, Palmeira das Missões-RS, 98300-000, Brazil
101 ^{tt} Fundação de Apoio à Pesquisa (FUNAPE), Universidade Federal de Goiás, Goiânia-GO,
102 74690-612, Brazil
103 ^{uu} Museu de Ciências Naturais, Universidade de Caxias do Sul, Caxias do Sul-RS, 95070-560,
104 Brazil
105 ^{vv} Foundation for Wildlife Conservation, Belize
106 ^{ww} Departamento de Meio Ambiente e Desenvolvimento, Universidade Federal do Amapá,
107 Macapá-AP, 68903-419, Brazil
108 ^{xx} Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural
109 Sciences, Umeå, Sweden
110 ^{yy} Department of Anthropology, Northern Illinois University, DeKalb, IL 60115
111 ^{zz} Department of Sociobiology and Anthropology, University of Göttingen, 37077 Göttingen,
112 Germany
113 ^{ab} Saint Louis Zoo, Saint Louis, MO 63110

114 ^{ac} The Aspinall Foundation, 101 Antananarivo, Madagascar
115 ^{ad} The Aspinall Foundation, Port Lympne Reserve, Hythe CT21-4LR, UK
116 ^{ae} Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation,
117 University of Kent, Canterbury CT2 7NZ, UK
118 ^{af} Instituto de Pesquisas Ecológicas (IPÊ), Nazaré Paulista-SP, 12960-000, Brazil
119 ^{ag} Estacion Biologica Corrientes (CCT Nordeste) – CONICET, Corrientes, W3401XAL,
120 Argentina
121 ^{ah} Association for Research and Conservation in the Amazon (ARCAmazon), Puerto Maldonado,
122 Madre de Dios, Peru
123 ^{ai} Junglekeepers Peru, Puerto Maldonado, Madre de Dios, Peru
124 ^{aj} Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85719
125 ^{ak} Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11790
126 ^{al} Omaha’s Henry Doorly Zoo and Aquarium, Omaha, NE 68107
127 ^{am} Animal Behavior Graduate Group, University of California, Davis, CA 95616
128 ^{an} Wildlife Conservation Society, La Paz, Bolivia
129 ^{ao} Red Boliviana de Primatología (RedBolPrim), Bolivia
130 ^{ap} Department of Forestry Engineering, Federal University of Viçosa, Viçosa-MG, 36570-900,
131 Brazil
132 ^{aq} Muriqui Instituto de Biodiversidade (MIB), Caratinga-MG, 35300-037, Brazil
133 ^{ar} Groupe d’Etude et de Recherches sur les Primates de Madagascar (GERP), 101 Antananarivo,
134 Madagascar
135 ^{as} School of the Environment, Portland State University, Portland, OR 97201
136 ^{at} Universidade Federal do Espírito Santo (UFES), Vitória-ES, 29075-910, Brazil
137 ^{au} Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E9, Canada
138 ^{av} Department of Anthropology, Kent State University, Kent, OH 44240
139 ^{aw} Centre for Social Sciences (Anthropology), Athabasca University, Athabasca, Alberta, T9S
140 3A3, Canada
141 ^{ax} Department of Biological Sciences, Southeastern Louisiana University, Hammond, LA 70402
142 ^{ay} Department of Migration, Max Planck Institute of Animal Behavior, 78315 Radolfzell,
143 Germany

144 ^{az} Smithsonian Tropical Research Institute, Panamá, 0843-03092, República de Panamá
145 ^{ba} Department of Behavioral Ecology, University of Goettingen, 37077 Goettingen, Germany
146 ^{bc} Research Group Primate Social Evolution, German Primate Center, Leibniz Institute for
147 Primate Research, 37077 Goettingen, Germany
148 ^{bd} Lemur Conservation Foundation, Myakka City, FL 34251
149 ^{be} Departamento de Ciencias de la Salud, Universidad Autónoma Metropolitana (UAM), Unidad
150 Lerma, México
151 ^{bf} Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional (CIIDIR),
152 Unidad Oaxaca, Instituto Politécnico Nacional, Oaxaca, México
153 ^{bg} Conservación de la Biodiversidad del Usumacinta A.C., Balancán, Tabasco, México
154 ^{bh} Department of Biology, University of Maryland, College Park, MD 20742
155 ^{bi} Mention Anthropobiologie et Développement Durable, Faculté des Sciences, University of
156 Antananarivo, 101 Antananarivo, Madagascar
157 ^{bj} Department of Mathematical Modelling of Social Systems, Institute for Research on Applied
158 Mathematics and Systems, Universidad Nacional Autónoma de México, Mexico City, México
159 ^{bk} Center for Complexity Sciences, Universidad Nacional Autónoma de México, Mexico City,
160 México
161 ^{bl} Graduate School of Asian and African Area Studies, Kyoto University, Kyoto, 615-8510,
162 Japan
163 ^{bm} Instituto de Investigaciones en Comportamiento Alimentario y Nutrición, Universidad de
164 Guadalajara, México
165 ^{bn} Department of Life Sciences, Imperial College London, London SW7 2AZ, UK
166 ^{bp} Instituto de Desenvolvimento Sustentável Mamirauá, Tefé-AM, 69553-225, Brazil
167 ^{bq} Département Sciences de la Nature et de l'Environnement, Facultés des Sciences, Université
168 d'Antsiranana, 201 Antsiranana, Madagascar
169 ^{br} College of Veterinary Medicine, Cornell University, Ithaca, NY 14853
170 ^{bs} Primate Research Institute, Kyoto University, Aichi 484-8506, Japan
171 ^{bt} Department of Anthropology, University of Colorado-Boulder, Boulder, CO 80302
172 ^{bu} Department of Anthropology, California State University, Sacramento, Sacramento, CA 95819

173 ^{bv} Interdepartmental Doctoral Program in Anthropological Sciences, Stony Brook University,
174 Stony Brook, NY, 11794
175 ^{bw} Red de Biología y Conservación de Vertebrados, Instituto de Ecología AC, Xalapa, Veracruz,
176 México
177 ^{bx} Neotropical Primate Conservation, Seaton, Cornwall PL11 3JQ, UK
178 ^{by} Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Federal do Mato
179 Grosso, Cuiabá-MT, 78060-900, Brazil
180 ^{bz} School of Life Sciences, Anglia Ruskin University, Cambridge CB1 1PT, UK
181 ^{ca} Instituto de Investigaciones Sociológicas de la Universidad Autónoma Benito Juárez de
182 Oaxaca, Oaxaca, México
183 ^{cb} Departamento de Zoologia, Universidade Federal de Pernambuco, Recife-PE, 50670-901,
184 Brazil
185 ^{cd} Laboratório de Ecologia, Comportamento e Conservação (LECC), Universidade Federal de
186 Pernambuco, Recife-PE, 50670-901, Brazil
187 ^{ce} Laboratório de Produtos Naturais e Espectrometria de Massas (LaPNEM), Faculdade de
188 Ciências Farmacêuticas, Alimentos e Nutrição (FACFAN), Universidade Federal de Mato
189 Grosso do Sul (UFMS), Campo Grande-MS, 79070-900, Brazil
190 ^{cf} Universidade Federal de Mato Grosso do Sul (UFMS), Campo Grande-MS, 79070-900, Brazil
191 ^{cg} Department of Biology, Institute of Zoology, Universität Hamburg, 20146 Hamburg, Germany
192 ^{ch} Biology Department, California Lutheran University, Thousand Oaks, CA 91360
193 ^{ci} Department of Anthropology, University of Wisconsin-Madison, 1180 Observatory Drive,
194 Madison, WI 53706
195 ^{cj} Department of Behavioral Sciences, San Diego Mesa College, San Diego, CA 92111
196 ^{ck} Departamento de Ciências Ambientais, Lab Ecologia e Conservação da Natureza and the
197 Programa Análise Ambiental Integrada, Universidade Federal de São Paulo, São Paulo-
198 SP, 04040-003, Brazil
199 ^{cl} Instituto Pró-Muriqui, São Paulo-SP, Brazil
200 ^{cm} School of Anthropology, University of Arizona, Tucson, AZ 85719
201 ^{cn} Facultad de Ciencias Forestales (FCF), Universidad Nacional de Misiones (UNaM), Eldorado,
202 Misiones, Argentina

203 ^{co} Instituto de Biología Subtropical (IBS), Consejo Nacional de Investigaciones Científicas y
204 Técnicas (CONICET), Puerto Iguazú, Misiones, Argentina

205 ^{cp} Asociación Civil Centro de Investigaciones del Bosque Atlántico (CeIBA), Puerto Iguazú
206 (3370), Misiones, Argentina

207 ^{cq} Department of Anthropology, University of Florida, Gainesville, FL 32603

208 ^{cr} Department of Anthropology, University of Austin at Texas, Austin, TX 78712

209 ^{cs} Wildlife Conservation Society, Bronx, NY 10460

210 ^{ct} Department of Anthropology, Stony Brook University, Stony Brook, NY 11794

211 ^{cu} Centre ValBio, Ranomafana, Madagascar

212 ^{cv} Department of Biology and Biotechnology “Charles Darwin”, Sapienza University of Rome,
213 00185 Rome, Italy

214 ^{cw} Facultad Maya de Estudios Agropecuarios, Universidad Autónoma de Chiapas, Catazajá,
215 Chiapas, México

216

217 ¹ To whom correspondence may be addressed. **Email:** teppley@sdzwa.org

218 ² Contributed equally to this work

219

220 **Author Contributions:** T.M.E., K.H., A.A.B., P.C.W., G.D., and L.S. designed research. T.M.E.,
221 C.A.C., J.U.G., M.A.O., D.B.A., N.A., K.R.A., M.A.A., J.F.A., A.L.B., M.B., J.C.B.M., M.B.,
222 S.A.B., M.B., D.C., C.C.M., C.J.C., M.C., F.A.C., T.S.C., X.C.P., J.C., O.M.C., C.C.K., I.C.C.,
223 B.D., C.D., K.M.E., E.M.E., K.J.E.E., L.M.F., A.M.F., R.G.F., C.F., M.L.F., I.P.F., V.B.F., I.F.,
224 D.G., G.B.G., K.S.H., E.W.H., R.R.H., S.M.H., M.T.I., S.E.J., P.M.K., E.A.K., T.K., C.K., F.K.,
225 M.M.K., L.R.L., M.E.L., E.E.L., M.C.L., J.M., A.D.M., F.R.M., T.H.M., M.S.M., L.S.M.,
226 L.A.M., C.B.M., M.B.N.R., M.A.N., H.N., M.T.O., J.O., E.R.P., M.S.M.P., B.P.G., L.M.P.,
227 G.P.M., B.E.R., V.R., N.A.R., Z.R., G.R.F., D.C.R., J.R., M.R., J.R., T.P.R., N.R., N.M.R.,
228 J.R.G., J.S., N.S., H.S., M.L.S., C.J.S., J.C.S.S., S.S., P.G.A.S.L., A.C.S., S.E.S.A., J.P.S.A.,
229 V.K.S., K.J.E.S., A.I.S., K.B.S., S.A.S., M.T., S.R.T., M.P.T., K.V., S.V.B., N.V., R.B.W.,
230 G.W., P.C.W., and G.D. contributed datasets. T.M.E., S.H., G.D., and L.S. analyzed data.
231 T.M.E., S.H., G.D., and L.S. wrote the paper. All authors read and edited this manuscript.

232

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237

238 **This PDF file includes:**

239 Main Text

240 Figures 1 and 2

241 Table 1

242

243 **Abstract**

244 Among mammals, the order Primates is exceptional in having a high taxonomic richness where
245 the taxa are arboreal, semi-terrestrial, or terrestrial. Though habitual terrestriality is pervasive
246 among the apes and African and Asian monkeys (catarrhines), it is largely absent among
247 monkeys of the Americas (platyrrhines), as well as galagos, lemurs, and lorises (strepsirrhines),
248 which are mostly arboreal. Numerous ecological drivers and species-specific factors are
249 suggested to set the conditions for an evolutionary shift from arboreality to terrestriality, and
250 current environmental conditions may provide analogous scenarios to those transitional periods.
251 Therefore, we investigated predominantly arboreal, diurnal primate genera from the Americas
252 and Madagascar that lack fully terrestrial taxa, to determine whether ecological drivers (habitat
253 canopy cover, predation risk, maximum temperature, precipitation, primate species richness,
254 human population density, and distance to roads) or species-specific traits (body mass, group
255 size, and degree of frugivory) associate with increased terrestriality. We collated 150,961
256 observation hours across 2,227 months from 47 species at 20 sites in Madagascar and 48 sites in
257 the Americas. Multiple factors were associated with ground use in these otherwise arboreal
258 species, including increased temperatures, a decrease in canopy cover, a dietary shift away from
259 frugivory, and larger group size. These factors mostly explain intra-specific differences in
260 terrestriality. As humanity modifies habitats and causes climate change, our results suggest that

261 species already inhabiting hot, sparsely canopied sites, and exhibiting more generalized diets, are
262 more likely to shift towards greater ground use.

263

264 **Significance Statement**

265 Primates from the Americas and Madagascar are predominantly arboreal but occasionally
266 descend to the ground. This increased ground use was associated with multiple ecological
267 drivers, including increased temperatures and a decrease in canopy cover, as well as species-
268 specific traits, including a dietary shift away from fruits and larger group size. As anthropogenic
269 impacts to habitats and climate worsen, our results suggest that diurnal species already inhabiting
270 hot, sparsely canopied sites, and exhibiting more generalized diets, are more likely to shift
271 towards greater ground use.

272

273 **Main Text**

274 **Introduction**

275 Eutherian mammal radiations are characterized by multiple evolutionary transitions
276 between terrestrial, arboreal, fossorial, and aquatic lifestyles (1, 2). In primates, arboreality is
277 hypothesized to be the ancestral condition (2-5). The evolutionary shift in some primate lineages
278 to terrestrial niches is associated with various morphological/skeletal adaptations (6-10).
279 Terrestriality is the prevalent strategy among some lineages of Catarrhini primates (i.e., African
280 and Asian monkeys and great apes; 9, 11). Conversely, adaptations for predominantly terrestrial
281 lifestyles are notably absent among living Platyrrhini of the Americas and Strepsirrhini of Africa
282 (including Madagascar) and Asia (7, 12-14). However, some of these arboreal, diurnal primates
283 periodically use the ground (15-21).

284 The evolutionary transition from arboreality to terrestriality is complex and carries
285 debated costs and benefits (22, 23), of which three main areas are discussed. First, descending to
286 the ground may come at the cost of greater predation risk (24, 25). Yet, it is unclear whether
287 arboreal or terrestrial lifestyles are characterized by greater predation risks (22, 23, 26-28).
288 Regardless, ground use by arboreal primates exposes them to novel predators and predation
289 patterns. Recent natural and anthropogenically driven ecological changes, however, negatively
290 impact native carnivore occupancy (29, 30), and may reduce terrestrial predation risk and, thus,
291 facilitating ground use in primates (17, 20, 31-33). It should be noted, however, that native
292 carnivores are often supplanted by non-native carnivores, including dogs, which can have a
293 negative impact on primate populations (29, 34, 35). Second, species occurring in naturally open
294 canopy habitats have been shown to use the ground frequently (36). To such a degree,
295 environmental changes and increasing anthropogenic encroachment on tropical forests may act
296 as catalysts for species to adopt terrestrial habits as canopy cover becomes patchy and forest
297 fragments provide fewer or lower quality resources. As a result, species may descend to the
298 ground to cross open areas more frequently to fulfil their energetic requirements, access
299 reproductive opportunities, or to disperse (17, 32, 37, 38). Therefore, plasticity in use of
300 additional ecological niches (e.g., terrestrial stratum) may enhance resilience to disturbance and
301 persistence in some fragmented landscapes (39, 40, 41). Third, extreme temperatures limit
302 species' biological functions (42, 43). As the understory and terrestrial environments are cooler
303 than the upper canopy (43, 44), intense seasonal heat in previously dense tropical forest
304 environments may drive arboreal species to seek thermoregulatory relief on the ground (45, 46).
305 Arboreal primates during hot periods regularly descend to the ground to access terrestrial water
306 sources for drinking or immersive cooling (18, 38, 47-51), and this behavior may become

307 increasingly common given the cascading impacts of climate change (e.g., extreme heatwaves
308 and droughts; 52, 53).

309 Primate community structure may also play an important role leading to terrestriality.
310 Typically, sympatric species maintain separate niches to reduce ecological competition (54, 55).
311 Therefore, in sites with high primate species richness (i.e., number of species) and greater
312 potential for interspecific competition, species that can expand into terrestrial niches may
313 experience reduced competition. As sympatric competitors, including other primate species, are
314 potentially crowded into smaller ranges due to habitat losses, interspecific competition may
315 increase until a new state is reached (56).

316 Species-specific factors have also been suggested to facilitate niche transition. Limited
317 resource availability in the canopy may lead to shifts in foraging strategies (57), including
318 increased terrestriality (11, 16, 38). For instance, arboreal species reliant on seasonal resources
319 may be more inclined to expand their dietary niche to include ground-based resources during
320 periods of food scarcity (33). Furthermore, fully or semi-terrestrial primates tend to be larger
321 than strictly arboreal primates and tend to live in larger groups (22, 58, 59). Both characteristics
322 are likely adaptations to high predation pressure and resource availability (59-63) and may have
323 facilitated the shift to terrestriality. Additionally, quadrupedal locomotion along the forest
324 canopy, which mainly includes largely horizontal substrates, may have selected for hind- and
325 forelimbs of similar length (7). This is in contrast to species using vertical clinging and leaping
326 locomotion from vertical substrates, which is associated with much longer hindlimbs (7). Species
327 in the former category are predicted from a biomechanical perspective to have more effective
328 cursorial quadrupedalism in a terrestrial environment (8, 64). Such species-specific factors may
329 have facilitated the evolutionary transition of some primates to terrestrial lifestyles (9, 11, 65).

330 We focus on diurnal primates of the Americas and Madagascar to explore anthropogenic
331 and ecological factors, and species-specific traits that are associated with greater use of the
332 ground in two independent radiations. We did not include monkeys and apes from Africa and
333 Asia as many of these species regularly exhibit semi-terrestrial and/or terrestrial lifestyles (9,
334 11), and thus they experienced their niche transition presumably millions of years ago.
335 Specifically, we are not interested in testing adaptations to terrestriality, but rather in the
336 ecological, anatomical, and behavioral traits that make terrestriality a possible option for an
337 arboreal primate. Regarding ecological and anthropogenic factors, we predict that terrestriality
338 will be greater in species at sites 1) where fewer native terrestrial predators pose a risk; 2) with
339 more open, degraded, or fragmented forest areas, (i.e., less canopy cover); 3) with higher
340 maximum temperatures favoring behavioral thermoregulation; 4) with high primate species
341 richness, and 5) in greater distance from both roads and areas of higher human population
342 densities (Fig. 1). Considering species-specific traits that may promote ground use, we predict
343 that terrestriality will be greater in species 1) that rely less on a diet of fruit as folivores tend to
344 have gut adaptations more suitable for terrestrial resources; 2) with larger bodies; 3) that form
345 larger groups; and 4) that exhibit anatomical adaptations for arboreal quadrupedalism (Fig. 1).

346

347 **Results**

348 The 47 arboreal diurnal primate species we studied spent little time on the ground ($2.5 \pm$
349 0.1% of the activity budget, monthly mean \pm SE; $N = 2,227$ months), and for over half of the
350 species (61.7%) terrestrial behavior comprised less than 1% of their total monthly activity.
351 Lemurs spent $4.8 \pm 0.3\%$ (monthly mean \pm SE; $N = 1,002$ months) of their time on the ground,
352 whereas platyrrhine monkeys spent $2.4 \pm 0.2\%$ (monthly mean \pm SE; $N = 1,225$ months) of their

353 time on the ground. Lemurs were on average more terrestrial than platyrrhine monkeys (Table 1;
354 SI Appendix, Table S2).

355 In the complete model, which accounts for both intra- and interspecific variability, the
356 most important ecological pressure positively associated with terrestriality was maximum
357 temperature, while habitat canopy cover was negatively associated with time spent on the ground
358 (SI Appendix, Table S2 and Fig. S8). Considering anthropogenic factors, distance to roads was
359 positively associated with ground use (SI Appendix, Table S2 and Fig. S8). For species-specific
360 factors, a species' degree of frugivory was negatively associated with terrestriality, whereas
361 larger group size was positively associated with terrestriality (SI Appendix, Table S2 and Fig.
362 S8). Furthermore, post-habituation time was negatively associated with ground use, meaning that
363 species studied across a greater number of months were less likely to exhibit terrestriality (SI
364 Appendix, Table S2 and Fig. S8).

365 For the within-species model, which evaluates the variability among conspecific
366 populations (Table 1; SI Appendix, Fig. S9), multiple ecological pressures influenced primate
367 ground use. Similar to the complete model, maximum temperature and distance to roads were
368 positively associated with terrestriality, while habitat canopy cover was negatively associated
369 with terrestriality. Unlike the complete model, however, terrestriality decreased with increasing
370 terrestrial predation risk, and increased with primate species richness. We also found a positive
371 interaction between primate-rich habitats and habitat canopy cover, indicating an amplified effect
372 of canopy cover on terrestriality in areas with higher primate species richness. Like the complete
373 model, the three species-specific factors related to terrestriality were degree of frugivory
374 (negative), group size (positive), and post-habituation (negative).

375 In the between-species model, which measures variability across species (Table 1; SI
376 Appendix, Fig. S10), none of the factors were strongly related to terrestriality. The only
377 ecological factor that exhibited a clear association was primate species richness (negative).
378 Species in habitats with denser canopy cover and with fewer sympatric primate species spent a
379 greater proportion of time on the ground. Terrestriality was positively related with body mass
380 and negatively with group size, indicating smaller species and larger groups, respectively,
381 spending more time on the ground.

382

383 **Discussion**

384 We found more terrestrial activity in hotter environments with more mammalian
385 predators, larger groups, and taxa with less frugivorous diets. However, the degree of
386 terrestriality varies both within and between species, and when this variation is analyzed
387 separately it reveals a more complex picture. Our within-species comparison shows that groups
388 living in more open habitats with more potential predators and richer primate communities
389 exhibit greater degrees of terrestriality. Species at more remote sites, i.e., greater distances from
390 roads, also spent more time on the ground. By comparison, our between-species analysis reveals
391 that species that descend more often to the ground tend to be smaller and live in larger groups.
392 Contrary to previous single-species studies that showed an observer effect (15, 39, 66, but see
393 33), shorter study duration (the number of post-habituation months) was strongly associated with
394 ground use.

395

396 *Ecological correlates to terrestriality*

397 Maximum temperatures showed a positive relationship with the time spent on the ground
398 on both the complete and intraspecific models, while our proxy for seasonality (i.e., monthly
399 precipitation) was not influential within any of the models. Gradual and rapid temperature
400 increases correlates with behavioral shifts (cf. 67, 68). A possible explanation is that lemurs and
401 platyrrhine monkeys increase their use of the ground as an adaptive thermoregulation strategy
402 (69, 70). For example, we found that primate species like *Eulemur fulvus* and *E. rufifrons* spent
403 considerably more time on the ground in relatively hotter tropical deciduous forest habitats of
404 Madagascar compared to their conspecifics inhabiting the cooler humid forest habitats, likely to
405 access terrestrial water sources (50). This finding supports the idea that shifting between
406 arboreality and terrestriality is an effective thermoregulatory response, with important
407 implications considering current global warming trends (52, 71, 72).

408 Canopy cover has long been considered a factor in many evolutionary shifts (73).
409 However, the degree to which this may result in a more terrestrial primate lifestyle is unclear
410 (11). Denser canopy cover was associated with spending less active time on the ground within-
411 species, but was not associated with ground use in the between-species model. The former is in
412 line with our expectation that terrestrial activity tends to be higher in habitats with sparser
413 canopies, such as those disturbed by anthropogenic activities (19, 38). Arboreal species in more
414 open habitats (i.e., sparser canopies) may need to descend to the ground to forage and drink (19,
415 34, 38, 74, 75), though their ability to do so may be guided by species-specific characteristics
416 acting as a predisposition, i.e., behavioral and anatomical exaptations (76, 77).

417 Primate species richness had contrasting results, with a negative effect on terrestriality in
418 the interspecific model and positive effect in the intraspecific model. As all primates within the
419 communities examined are arboreal, greater numbers of species at a site may lead to higher

420 competition for canopy resources, including both food and space. Under specific circumstances,
421 descending to a rarely exploited niche (the forest floor) may be critical for coping with periods of
422 limited resources (78). The positive interaction effect between canopy cover and primate species
423 richness in the intraspecific model supports our hypothesis. Essentially, the negative effect of
424 canopy cover on terrestriality was weaker as sympatric taxa richness increased. In other words,
425 when canopy cover increases, the decrease in terrestriality is less pronounced in habitats with
426 high primate diversity where we would expect higher competition. However, it is possible that at
427 sites where a species may have recently become locally extirpated, this loss may result in
428 competitive release, allowing one or more of the remaining species to partially, or fully, exploit
429 newly available resources (79-81). Compared to many mammal taxa, primates tend to exhibit a
430 high degree of behavioral flexibility (82-83), and interindividual variation may be the
431 mechanism underlying niche expansion (84).

432 Predation pressure is difficult to quantify and evaluate. The number of potential predator
433 species provides a proxy with which to measure this risk (85, 86), and some site-/species-focused
434 studies have noted that relaxation of predation pressure led to more ground-based activity (20,
435 32, 39). Interestingly, terrestrial predator species richness was associated with more terrestrial
436 activity in our within-species model. Though we were unable to account for predator population
437 abundance or the potential ecological and co-occurrence factors affecting these taxa (87), it
438 appears that anthropogenic factors may play a role. Human population density and distance to
439 roads may be considered as general proxies for various aspects of human encroachment,
440 including feral dogs (*Canis familiaris*) which are known to prey upon wildlife (34, 35, 74). Of
441 the two anthropogenic factors, conspecifics were more terrestrial at sites further away from
442 roads.

443

444 *Species-specific factors as potential facilitators of terrestriality*

445 Frugivory was associated with decreased ground use in both the complete and
446 intraspecific models, supporting previous assertions that diet is a driving force of terrestriality
447 (38, 88). This link may be associated with folivores or species with a broad dietary spectrum
448 using the ground more often to forage on different preferred foods (17, 89), and/or because they
449 have gastrointestinal and dental adaptations allowing them to more efficiently use terrestrial
450 resources (90). Despite the general reduced ground use by frugivores, periods of reduced fruit
451 availability may lead facultative frugivores to search the ground for novel food resources to meet
452 their seasonal nutritional needs (21, 91, 92). Many primates with broad dietary niches come to
453 the ground to engage in geophagy and to access mineral licks (93, 94) and potentially fermented
454 foods (95). However, given the supplementary nature of this feeding habit (96) that often
455 involves short terrestrial travel, it has not been considered a key causative factor in any major
456 shift in strata use. Primates may also descend to the ground to forage for arthropod prey (19, 21).

457 Group size had an effect in both the complete and within-species models. Large groups
458 can facilitate terrestriality as they can potentially reduce predation risk. Folivores are in principle
459 less constrained by group size compared to frugivores due to the less clumped spatiotemporal
460 availability of preferred resources, though this is not always the case (97, 98). However, though
461 it is conceivable that large groups foster terrestrial activity, it is also possible that groups that use
462 the ground more often tend to form larger groups to reduce predation risk, leaving the causal
463 relationship unclear. In both *Brachyteles hypoxanthus* in Caratinga (Brazil) and *Hapalemur*
464 *meridionalis* in Mandena (Madagascar), it was the case that the largest group was considerably
465 more terrestrial than smaller groups (17, 39).

466 Biomechanical, e.g., size-related and anatomical, challenges may impose various
467 biological, ecological, and physiological constraints within both the arboreal and terrestrial strata
468 (8). Such morphological factors could be species-specific consequences that evolve after, or in
469 parallel with, the initial niche expansion into terrestrial activity. However, contrary to our
470 hypothesis, we found a negative effect of body mass between species (i.e., smaller species
471 showed increased terrestriality). Original hypotheses about the relationship between body size
472 and terrestriality proposed by Fleagle (7, 59) were developed to explain the range of niche use in
473 the entire Primate Order, including the larger-bodied catarrhines. The primates included in this
474 study, platyrrhines and lemuriformes, represent a more restricted range of body mass variation,
475 and therefore it is possible that a different relationship between terrestriality and body mass is
476 present for the entire Order. We cannot evaluate the role that the relatively recent extinction of
477 the larger and more terrestrial lemur species (99) may have had in releasing the competition for
478 terrestrial resources with the extant smaller lemur species.

479 Though post-habitation months was used to control for a possible positive observer
480 effect, our complete and within-species model showed that primates studied for shorter periods
481 more strongly associated with ground use. While this contrasts from some single-species studies
482 (15, 39, 66), we believe our negative effect is more likely the result of the non-random
483 distribution of study periods with respect to seasons and/or the non-random distribution of
484 species with respect to their average level of arboreality within our dataset.

485

486 *Conclusion*

487 We have shown that there are multiple factors that may lead arboreal primates to use the
488 ground and that this transition is influenced by site-specific ecological pressures. Specifically,

489 habitats with sparser canopies may be responsible for the evolutionary transition of non-human
490 primates to terrestrial lifestyles (11, 19), whereas the more proximate causes of strata shift appear
491 to be hotter environmental conditions (72) and dietary shifts away from frugivory. Considering
492 species-specific traits, larger groups and smaller body mass facilitated ground use.

493 Although significant climate changes in both the Americas (100) and Madagascar (101) likely
494 facilitated faunal turnover and speciation, it is not clear why terrestriality did not evolve there to
495 the same extent as it is seen in catarrhines. Fossil records are sparse and the real extent of niche
496 diversification that occurred in lemurs and platyrrhines over their evolutionary history is far from
497 being understood (7). Examining primate behavioral and ecological flexibility alongside current
498 environmental conditions, however, provides insight into evolutionary transitional periods that
499 resulted in shifts to novel ecological niches. As human activity drives climate change, degrades
500 primate habitats, and shifts plant phenological patterns, primate populations are facing
501 unprecedented challenges that threaten their persistence (52, 71, 102-105). We expect that an
502 increased use of the ground strata by species inhabiting hot, sparsely canopied sites and that
503 exhibit a more generalized diet, can buffer species against extinction. Productive future lines of
504 research that will further clarify factors driving the evolution of terrestriality include comparing
505 behavioral repertoires in terrestrial versus arboreal environments, evaluating potential ecological
506 and life history drivers of annual variation in terrestrial behaviors, and if habitat structure
507 explains variation in population-level terrestriality. All non-human primates, however, will be
508 faced with challenges created by anthropogenic changes and for species less inclined to
509 terrestrial activity, fast and effective conservation strategies will need to be implemented to
510 ensure their survival.

511

512 **Materials and Methods**

513 Co-authors contributed raw monthly behavioral ecology data from 47 primate taxa,
514 specifically 15 lemur species representing two families (Lemuridae and Indriidae), and 32
515 platyrrhine species representing four families (Atelidae, Callitrichidae, Cebidae, and Pitheciidae)
516 (Dataset S1). This collated dataset includes 150,961 observation hours across 2,227 months from
517 species at 68 research sites, specifically 20 sites in Madagascar and 48 sites throughout the
518 Americas (Fig. 2; SI Appendix, Table S1). Our dataset includes 16 primate species (specifically
519 10 lemur and six platyrrhine monkey species) for which we have data from multiple sites.

520 For each species, we provide monthly proportional data to account for different data
521 collection methods used in each study. Since nocturnal species are exposed to different
522 ecological pressures compared to diurnal primates, we only focused on diurnal primates.
523 Datasets included had a minimum of 12 hours/month to increase the chances that rare events, in
524 our case terrestriality by arboreal species, would be recorded (106). We considered the monthly
525 proportion of time spent terrestrially as our dependent variable.

526

527 *Ecological drivers*

528 We extracted site- and time-specific climate and habitat values in Google Earth Engine
529 (earthengine.google.com) using the spatial coordinates and the year and month of the
530 observations (107). We extracted monthly maximum temperatures and monthly total
531 precipitation from the *ERA5 Monthly Aggregates* dataset (108). The latter is used as a
532 conservative proxy for seasonality (109), incorporating the rainfall variation at research sites for
533 the months included in our dataset. We obtained the relative canopy cover using a circular buffer
534 around the coordinates of each study site from the Landsat Tree Cover Continuous Fields

535 (GLCF) dataset (110; SI Appendix, Fig. S1). Specifically, the buffer area was equal to twice the
536 size of each study species reported mean home range area.

537 We estimated the number of potential terrestrial mammalian predators per species per site
538 from the number of carnivore species per location using IUCN range maps (111). For each
539 species per location, we only considered predators with a mean body mass greater than or equal
540 to $\frac{1}{4}$ of the mean body mass of the focal primate. This ratio was based on the minimum predator-
541 prey ratio observed in terrestrial mammals (Appendix S1 in 112). The body mass threshold is
542 very conservative and may lead to the inclusion of species that do not typically prey on adult
543 primates; however, considering primates' slow life histories and the additive risks to
544 juveniles/infants, smaller predators can potentially trigger a fear reaction (113, 114). This
545 approach is also limited by the nature of IUCN range maps and the consideration of predator-
546 prey body mass ratios, which likely overestimates the presence of predators as large predators
547 may have been extirpated by local hunting and habitat loss. However, this approach allows us to
548 estimate the spatial gradients of predator species richness at this scale of analysis for all sites and
549 species, thereby avoiding potential author or publication reporting biases (cf. 115). Although
550 primates may also be preyed upon by birds of prey, snakes, and other primates, carnivores are
551 considered their main terrestrial predators (116, 117).

552 Using IUCN range maps (111), we also estimated the number of sympatric primate
553 species per site, i.e., species richness (SI Appendix, Figs. S2 and S3). Given the potential
554 increased effect of interspecific competition in sites with less canopy cover (potentially more
555 fragmented), we examined the interaction between these two factors.

556 Finally, we considered two proxies of anthropogenic disturbance: human population
557 density and distance to roads. The former accounts for the number presence of humans, whereas

558 the latter is a proxy of inverse of remoteness (i.e., inverse of accessibility to humans). We
559 obtained the human population density data from the Socioeconomic Data and Applications
560 Center (<http://sedac.ciesin.columbia.edu/>). We used the Gridded Population of the World (GPW)
561 dataset, v.4 dataset (118) for 2000, 2005, 2010, 2015, and 2020 at 30 arc-second resolution
562 (~1km) (SI Appendix, Figs. S4 and S5). We matched the terrestriality data with the values of
563 human population density using the closest layer in time. Road data for the countries of interest
564 were extracted from the OpenStreetMap database (openstreetmap.org). From the vector files we
565 only retained primary, secondary, and tertiary roads, motorways, trunks, all related "links", and
566 residential roads. Instead, we excluded all unclassified roads, paths, footways, and similar. We
567 then rasterized the vector layer at 1km resolution and calculated the distance from the nearest
568 road for the entire study area (SI Appendix, Figs. S6 and S7). All raster data processing was
569 conducted in R version 3.6.3 (119) using ‘raster’ package (120).

570

571 *Species-specific factors*

572 For each species’ specific site, co-author(s) contributed the monthly proportion of time
573 spent feeding on fruit, the mean body mass and the mean group size measured in the field. In the
574 absence of mean body mass, we used data from the ‘All the World's Primates’ database (121).
575 We inferred locomotion type via the Inter-Membral Index (IMI; 64), which is calculated as
576 $((\text{length of humerus} + \text{length of radius}) / (\text{length of femur} + \text{length of tibia})) * 100$. Quadrupedal
577 primates typically have an IMI between 67 and 104; of the arboreal quadrupeds, those falling
578 below the lower threshold typically exhibit vertical clinging and leaping (VCL), and those above
579 the upper threshold are typically categorized as exhibiting brachiation, but also suspensory
580 locomotion (7, 8, 64). Given potential for error when collecting field measurements, and the

581 relative stability of the IMI within genera, we assigned each species to a category based on the
582 IMI averaged at the genus level.

583

584 *Statistical analyses*

585 We tested our hypotheses by fitting a zero-inflated model with a beta family and logit
586 link-function and using Bayesian inference. The use of a zero-inflation and beta family allowed
587 accommodating for the highly skewed and zero-inflated distribution of terrestriality values
588 bounded between 0 and 1. We added a group level to study site and one to species to control for
589 multiple estimates in the same locations and multiple estimates per species, respectively.
590 Considering climatic variation and its effect on resource phenology (122), we controlled for
591 seasonality using monthly temperature and total precipitation at each site. We used study
592 duration (i.e., the number of months post-habitation) to control for observer effect within the
593 models. We controlled for phylogenetic effects by using a variance-covariance matrix derived
594 from the phylogeny in Upham et al. (123). An additional observation level random effect was
595 added to control for overdispersion. All fixed factors were scaled to a mean of zero and standard
596 deviation of 1 to ensure comparability of the effect sizes, as well as improving numerical
597 stability in their estimation. We used weakly informative priors using a normal distribution with
598 a standard deviation of 10 for the intercept, and a standard deviation of 1.5 for all slope
599 coefficients, thereby limiting the range to a plausible gradient of variation considering the logit
600 link-function and scaled coefficients (124). All predictors were tested for multi-collinearity prior
601 to the modelling but none showed a correlation coefficient >0.7 , so all variables were retained in
602 the final model (125).

603 The complete model accounted for both intra- and interspecific variability in
604 terrestriality, thus, we ran two additional models to disentangle the variability within- and
605 between-species. To assess whether the detected effects could also explain the different degrees
606 of terrestriality among conspecific populations (within-species model), we included only
607 anthropogenic and ecological drivers, as well as site-specific species' factors for which we had
608 data (% frugivory and group size). Prior to fitting this second model, we first subtracted the
609 species' mean from each observation value (species mean deviation) (126). Then, we fitted a
610 model including both ecological drivers and species-specific traits to estimate the variability
611 across species (between-species model), from which we subtracted the species mean deviation
612 from each observation value. For both the within- and between-species model, we rescaled the
613 variable to a mean of zero and standard deviation of 1 prior to model fitting and used the same
614 weakly informative priors used for the complete model.

615 We ran 6,000 iterations over 10 Markov Chain Monte Carlo chains for each model, with
616 a 'burn in' period of 2,000 iterations per chain leading to a total of 40,000 usable posteriors. We
617 also checked models for chain convergence and parameter identifiability. We summarized the
618 posterior distributions of coefficient estimates using 95% credible intervals. We considered
619 credible intervals that did not overlap with zero as strong evidence of directionality. We also
620 reported the probability of direction, a threshold-independent measure of evidence that varies
621 from 50% to 100% and that indicates the probability of a coefficient being different from zero
622 (127). We fitted the models in R version 3.6.3 (119) using the 'brms' package (128), for model
623 fitting, 'bayestestR' (127) for Bayesian summary statistics, and 'ape' (129) and 'phytools' (130)
624 for handling the phylogenetic data. All statistical codes used in the analyses are available via
625 Figshare (<https://doi.org/10.6084/m9.figshare.19344992.v1>).

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1151 **Figure legends**

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1154 **Fig. 1.** Hypothesized relationships between species-specific traits, and ecological and
1155 anthropogenic factors and ground use by monkeys in the Americas and lemurs in Madagascar,
1156 and not any specific transition in one species or another. For species-specific traits, taxa
1157 exhibiting quadrupedal locomotion (inferred from their inter-membral index), have a larger
1158 group size, and have greater body mass are hypothesized to use the ground more. Taxa with diets
1159 consisting of more fruit, and exhibiting vertical clinging and leaping (VCL) and brachiator
1160 locomotion (inferred from their inter-membral index) are hypothesized to spend less time on the
1161 ground. Regarding ecological factors, taxa inhabiting sites with higher maximum temperatures
1162 and greater primate species richness are hypothesized to use the ground more. Taxa inhabiting
1163 sites with a greater number of terrestrial predators and greater continuous canopy coverage are
1164 hypothesized to spend less time on the ground. Regarding anthropogenic factors, taxa inhabiting
1165 sites that are further distances from roads are hypothesized to use the ground more, whereas taxa
1166 inhabiting sites that are closer to larger human population densities are hypothesized to spend
1167 less time on the ground.

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1170 **Fig. 2.** Spatial distribution of primate genera included in our behavioral ecology dataset.