

Failure to consider landscape complexity underestimates terrestrial animal home range size

Waldemar Ortiz-Calo (✉ waldemar.ortiz@umontana.edu)

University of Montana W A Franke College of Forestry and Conservation <https://orcid.org/0000-0002-3440-0163>

David R. Heit

University of New Hampshire

Robert A. Montgomery

University of Oxford Wildlife Conservation Research Unit

Research Article

Keywords: spatial dimensionality, home range estimation, landscape complexity, topography, terrestrial wildlife

Posted Date: March 7th, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1325043/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

1 **Failure to consider landscape complexity underestimates terrestrial animal**
2 **home range size**

3 WALDEMAR ORTIZ-CALO*¹, waldemar.ortiz@umontana.edu

4 DAVID R. HEIT², dh1157@wildcats.unh.edu

5 ROBERT A. MONTGOMERY³, robert.montgomery@zoo.ox.ac.uk

6 ¹ W.A. Franke College of Forestry and Conservation, Wildlife Biology Program, University of
7 Montana, Missoula, MT, United States

8 ² Department of Natural Resources and the Environment, University of New Hampshire, James
9 Hall, Durham, NH, 03824 USA.

10 ³ Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, The
11 Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Oxon OX13 5QL, U.K.

12 **Corresponding author: Waldemar Ortiz-Calo**, W.A. Franke College of Forestry and
13 Conservation, Wildlife Biology Program, University of Montana, Missoula, MT, United States.

14 ORCID: 0000-0002-3440-0163

15

16 **ABSTRACT**

17 **Context:** The measurement of home range size and configuration has been a powerful and
18 enduring method of quantifying animal-habitat relationships. Traditionally, home range
19 estimators have been built using bivariate location data (e.g., x-y coordinates) which inherently
20 assumes that animal movement is two-dimensional (2D). However, this is not representative of
21 real-world systems.

22 **Objectives:** Home range estimators that make these assumptions may underestimate animal
23 home range size where 2D+ movement is probable. Our objective is to evaluate if landscape
24 complexity impacts the accuracy of traditional home range estimators.

25 **Methods:** We randomly sampled 50,000 animal home range extents at four different spatial
26 scales (5, 10, 100, and 250 km²). We then quantified 2D and 2D+ home range estimates for each
27 home range extent and quantified landscape complexity within.

28 **Results:** When landscape complexity was low (i.e., global terrain ruggedness index [TRI] <
29 5.23) 2D and 2D+ home ranges were not statistically ($\alpha < 0.05$) different. However, when
30 landscapes were complex (i.e., $TRI \geq 5.23$), 2D home ranges significantly underestimated home
31 range area (range 5% to 83.66%). Importantly, 18% of the world's terrestrial surface exceeds
32 TRI level of 5.23.

33 **Conclusions:** We found that as landscape complexity increased, so did the percent difference
34 between 2D and 2D+ home range estimates across all spatial scales. We recommend that
35 landscape complexity should be considered when modeling animal home ranges. By doing so,
36 quantitative biases may be mitigated.

37 **Keywords:** spatial dimensionality, home range estimation, landscape complexity, topography,
38 terrestrial wildlife

39 INTRODUCTION

40 Rigorous research on animal movement and habitat use has been a cornerstone of
41 ecological inquiry for over a century (Grinnell 1917; Elton 1927). Within this context, home
42 range estimation has become a predominant tool for quantifying the spatio-temporal nature of
43 animal-habitat relationships (Powell and Mitchell 2012). Home ranges depict the post-natal area
44 that an animal uses to fulfill its life history requirements (Burt 1943). Integral to assessments of
45 animal ecology, initial efforts to quantify home range size and configuration often included
46 labor-intensive tracking of animals and the marking of resultant locations on paper maps
47 (Hamilton 1937; Blair 1942; Haugen 1942; Adams and Davis 1967). By the mid-20th century
48 however, telemetry technologies were being retrofitted to collect animal movement data
49 remotely (Adams 1965; Sanderson 1966; Benson 2010). Technologies then advanced from Very
50 High Frequency (VHF) to Global Positioning System (GPS) instruments that could capture
51 animal-habitat relationships at increasingly fine scales (Tomkiewicz et al. 2010). Such
52 technological developments led to concurrent growth in the quantitative tools used to estimate
53 animal movement and estimate animal home ranges (Worton 1987; Kie et al. 2010).

54 Today, there is a diversity of home range estimators including minimum convex
55 polygons (Schoener 1981), kernel density methods (Winkle 1975), Brownian-bridge movement
56 models (Horne et al. 2007), and autocorrelated kernel density approaches (Fleming et al. 2015),
57 among others. These techniques have, with time, been modified to account for various sources of
58 bias including sample size variation (Seaman et al. 1999), bandwidth optimization (Jones et al.
59 1996), fix rate (Kochanny et al. 2009), telemetry error (Montgomery et al. 2010), and temporal
60 autocorrelation (Hansteen et al. 1997). Interestingly, landscape complexity is a source of
61 potential bias that has yet to be widely addressed (Montgomery et al. 2020; Heit et al. 2021).

62 Presently, home range estimates tend to be predicted using bivariate location data (i.e. x-y
63 coordinates; Boulanger and White 1990). This analytical tendency inherently presumes that
64 animal movement occurs on a 2D, or flat, plane. In reality, most animals inhabit environments
65 with differing levels of complexity in landscape structure, a fact which is evident across scales of
66 animal-habitat relationships (Montgomery et al. 2020).

67 There are four spatial domains, including aquatic, aerial, subterranean, and terrestrial,
68 within which animal movement takes place (Montgomery et al. 2020). The mechanics of
69 movement within these domains, whether that be swimming, flying, burrowing, or walking,
70 depends, in part, on landscape complexity as represented by wind, currents, bathymetry,
71 topography, or other physical barriers. When navigating these landscape complexities, animals
72 use fractal dimensions that exceed 2D. These movements are thus referred to as 2D+
73 (Montgomery et al. 2020; Heit et al. 2021). Recent efforts in the aquatic and aerial spatial
74 domains, have been made to incorporate such spatial dimensionality into home range estimation
75 (May et al. 2008a; Nielsen et al. 2013; Cooper et al. 2015). Despite these advancements,
76 landscape complexity has been largely overlooked in the terrestrial spatial domain with <1% of
77 home range studies incorporating 2D+ movement into their calculations (Heit et al. 2021).
78 However, the consequences of these analytical tendencies largely remain unclear.

79 We designed a global simulation study to quantify the difference between home range
80 estimates built using traditional methods (i.e., 2D) to those that we designed to incorporate 2D+
81 animal movement. We hypothesized that 2D methods would underestimate home range size and
82 that the differences between 2D and 2D+ estimators would become more pronounced as
83 landscape complexity increased. Resolving this hypothesis would have important implications
84 not only for ecological research but also for conservation and management philosophies

85 informed by animal home range estimates. We simulated home range extents at four spatial
86 scales (5, 10, 100, and 250 km²), representative of terrestrial animals with varying body size and
87 ranging requirements (Meserve 1977; Zalewski et al. 2004; Kochanny et al. 2009). Once
88 simulated, we randomly selected 12,500 home range extents per spatial scale around the world
89 for a total of 50,000 simulations. Within these home range extents, we quantified 2D area
90 estimates, 2D+ area estimates, the percent difference between the two area estimates, and
91 landscape complexity as a function of terrain ruggedness index (TRI). Lastly, we quantified the
92 relationship of TRI and the percent difference between 2D and 2D+ area estimates and discuss
93 the ramifications for prevailing depictions of animal ecology. We also explore the implications
94 of our results for conservation and management actions built upon animal home range estimates.

95 **MATERIAL AND METHODS**

96 *Digital Landscape Creation*

97 To build our simulations, we first randomly selected 2,500 digital elevation models
98 (DEM) from the National Aeronautics and Space Administration's (NASA) Advanced
99 Spaceborne Thermal Emission and Reflections radiometer (ASTER) database. The ASTER
100 database geographically extends from 83° North to 83° South and consists of 22,912 raster tiles
101 at a 30 m resolution, each representing a one-degree by one-degree area of the Earth's terrestrial
102 surface. Digital Elevation Model databases often contain latitudinal distortions where raster cells
103 closer to the equator have a greater surface area than those nearer to the poles. Therefore, prior to
104 further analyses, we implemented a bilinear interpolation algorithm to standardize the resolution
105 of each raster to be 30 m so as to facilitate cross-tile comparisons.

106 Once standardized, we calculated four derivative layers for each of the rasters. The first
107 layer we created was a raster depicting the 2D surface area. Next, we created a 2D+ surface area
108 raster by implementing Jenness' tessellation algorithm on the DEM tile (Jenness 2004). This
109 algorithm estimates the 2D+ surface area of each cell by drawing a line from the centroid of the
110 cell to the centroid of its eight neighboring cells, thus forming eight distinct triangles. Using a
111 modified Pythagorean formula, we calculated the sum of the areas of the triangles which
112 ultimately depict a cell's surface area when accounting for elevational differences between it and
113 surrounding cells. We then quantified the percent difference in surface area between the 2D and
114 2D+ raster layers. Finally, we modeled landscape complexity as a function of the terrain
115 ruggedness index (TRI) algorithm using the raster package in R (Riley et al. 1999; Hijmans
116 2020) to quantify the implications of landscape complexity around the world. Once all four
117 layers were calculated, we compiled each into raster stacks for further analysis.

118 *Home Range Simulation*

119 Next, we simulated animal home range extents for each raster stack and at four spatial
120 scales (5, 10, 100, or 250km²) representative of terrestrial animals with varying body size and
121 ranging requirements by implementing a fishnet-based sampling approach (Meserve 1977;
122 Zalewski et al. 2004; Kochanny et al. 2009). This methodology consists of resampling rasters to
123 a user-defined resolution and applying a specified aggregation strategy to calculate the resulting
124 cell values. Using this technique, we resampled the rasters for the home range extents at the 5,
125 10, 100, or 250km² levels. We then randomly sampled five home ranges from each size category
126 around the world and iterated this process for each of the raster stacks. Due to the sampling
127 efficiency of raster stacks, each extent contained the home range's metadata information and its
128 respective values from each of the four derivative raster layers contained within the stack. Once

129 all home range estimates were sampled, we eliminated those that were randomly positioned over
130 bodies of water or those where the landscape complexity was unrealistic for animal occupation
131 (i.e., TRI values > 25). We note here that TRI calculations are resolution dependent. Thus, the
132 precise TRI values that we report are specific to a 30 m resolution DEM and will be different at
133 varying resolutions.

134 Lastly, we quantified the relationship between TRI and the percent difference between
135 2D and 2D+ home range estimates. We modeled this relationship using a generalized additive
136 model (GAM) in the R programming language (R Core Team 2020). With this model, we
137 identified the average levels of TRI needed to exceed our threshold of statistical significance ($\alpha <$
138 0.05). Once we identified this threshold, we calculated global levels of TRI at spatial resolutions
139 of 5, 10, 100, and 250km². With these calculations, we then quantified the proportions of the
140 Earth's terrestrial surface that were within or exceeded the threshold of statistical significance
141 (i.e., $\alpha < 0.05$).

142 **RESULTS**

143 We simulated 12,500 home range extents per spatial scale (5, 10, 100, or 250km²) for a
144 total of 50,000 simulations. Once we eliminated extents that did not meet our criteria (i.e.,
145 overlapping with water bodies or in TRI extremes), we had a total of 39,513 home range extents
146 with a mean of 9,878 samples per size category. The 2D home range estimates were, on average,
147 2.80% (SD = 0.57) smaller than the 2D+ estimates across all spatial scales (Table 1). This 2.80%
148 differential was detected when the home range estimates had an average TRI of 3.72 (SD = 0.03)
149 across spatial scales.

150 The difference between 2D and 2D+ home ranges was positively related to TRI (Fig. 1).
151 The average percent difference in the non-significant estimates was 1.1% (SD = 1.05).

152 Accordingly, these home range estimates had an average TRI value of 2.57 (SD = 1.28). The
153 remaining 16% ($n = 6,223$) of home range estimates, which experienced significant changes in
154 surface area, had an average percent difference of 12.3% (SD = 6.3) with an average TRI value
155 of 9.88 (SD = 2.93). Amongst these simulations, underestimation ranged from 5% to 83.66%.
156 Overall, a mean TRI value of 5.32 was the threshold for a significant difference between the 2D
157 and 2D+ home range estimates. Using the 5.32 TRI threshold level, we found that approximately
158 18% (e.g., 18.13% at 5 km², 18.04% at 10 km², 17.97% at 100 km², and 17.9% at 250 km²; Table
159 2) of the earth's surface had enough landscape complexity to yield a statistically significant
160 difference between 2D and 2D+ home range estimates (Fig. 2).

161 **DISCUSSION**

162 For three-quarters of a century, home range estimators have been a fundamental tool to
163 quantify the nature of animal-habitat relationships (Johnson 1980; Gompper et al. 2016).
164 Researchers have made considerable efforts to account for various sources of imprecision and
165 bias both in the collection and representation of animal locational data (Worton 1987; Kie et al.
166 2010; Heit et al. 2021). Our study demonstrates that landscape complexity continues to be an
167 important source of bias in terrestrial home range estimation. We found that when landscape
168 complexity is relatively high (i.e., TRI > 5.23 at a 30 m resolution), traditional techniques
169 underestimate home range size. More importantly, we found this relationship to scale across
170 animal body size and ranging requirements, at least for home ranges between 5 km² and 250
171 km². We also found that the amount of bias varied according to the degree of landscape
172 complexity within the home range extent. For instance, home range estimates built from
173 traditional techniques (i.e., 2D) were not statistically different from 2D+ estimators at low levels
174 of landscape complexity (i.e., TRI < 5.23 at a 30 m resolution). However, statistical differences

175 were evident beyond that level and differentials were as high as ~83% in highly complex
176 landscapes. This demonstrates that in many parts of the world and for many species of animal,
177 traditional estimators do not accurately quantify home range size (Fig. 2). We recommend that
178 researchers studying animals inhabiting complex landscapes should consider 2D+ estimation to
179 accurately quantify home range patterns. Furthermore, while home range estimation methods
180 will continue to be updated with time, we contend that a key part of this technological
181 progression must include landscape complexity.

182 Animals move about their landscapes navigating various tradeoff decisions according to
183 prevailing biotic and abiotic conditions (Sappington et al. 2007; Zhang et al. 2014; Kropil et al.
184 2015; Mckinney et al. 2016). For many species, landscape complexity plays a vital role in these
185 animal-habitat relationships. Animals may use complex landscapes for refugia, to acquire food,
186 mitigate climatic shifts, or ease intra-specific stressors, amongst others (Sappington et al. 2007;
187 Tracey et al. 2014; Farhadinia et al. 2019). Given the importance of these animal-habitat
188 relationships for survival and reproduction, the accuracy of the methods used to quantify these
189 relationships is, necessarily, high. There is good reason to believe that new ecological insights
190 will become possible via the incorporation of landscape complexity. For example, Farhadinia et
191 al. (2019) found that home range overlap of Persian leopards (*Panthera pardus saxicolor*) could
192 be explained by vertical partitioning amongst resident individuals. Furthermore, Farhadinia et al.
193 (2019) noted that due to high amounts of landscape complexity, home range estimates increased
194 by up to 38% when landscape complexity was incorporated into their calculations. Zhang et al.
195 (2014) observed that giant pandas (*Ailuropoda melanoleuca*) exhibited seasonal home range
196 shifts along an elevation gradient in mitigation of food shortages. These examples illustrate that

197 incorporating landscape complexity into animal-habitat relationships studies allowed for greater
198 insight to the spatial dynamics and resource use of study animals.

199 The accuracy of home range estimators is not only important for quantitative or applied
200 ecology, but is also crucial for conservation management decisions that are based on this science
201 (Husseman et al. 2003; Sappington et al. 2007; May et al. 2008b). With the dramatic loss of
202 biodiversity occurring around the globe, conservation efforts require the best available science to
203 inform decision making (Ripple et al. 2016). For example, the International Union for the
204 Conservation of Nature (IUCN) regularly conducts risk assessments for species around the
205 globe. These assessments consist of evaluating the viability and vulnerability of species based on
206 the IUCN's established criteria. Amongst these criteria, the extent of occurrence and area of
207 occupancy of a species is necessary to classify their status (IUCN Standards and Petitions
208 Committee 2019). These criteria can be informed by a number of data types, but home range
209 estimates are one of the most widely used. As demonstrated by our study, 2D estimators are
210 prone to underestimate the size of a home range in complex landscapes. At risk here is that
211 technological assumptions and analytical bias preventing the incorporation of 2D+ methods may
212 not provide an accurate depiction of the ranging requirements of species of conservation or
213 management concern. Thus, we contend that the consideration of landscape complexity is vital to
214 the appropriate conservation and management of terrestrial animals.

215 The impacts of landscape complexity were evident in our study across scales. Analytical
216 barriers prevented us from examining animal ranging patterns $< 5 \text{ km}^2$, but we expect these
217 comparable patterns would be detected at smaller scales. Traditional DEM datasets are often
218 limited to spatial resolutions that are too coarse (e.g., ASTER data) for species with smaller body
219 sizes. Researchers can justifiably use DEM data at a 30m^2 resolution to account for landscape

220 complexity for larger species. However, this same data cannot be used to account for the impacts
221 of landscape complexity on smaller species. That being said, advancements in telemetry
222 technology have made it possible to create monitoring devices as light as 1 gram. Considering
223 the guidelines of monitoring devices not exceeding 3-5% of an animal's body weight (Kenward
224 2000), scientists are able to monitor species that are as small as 20 grams. House mice (*Mus*
225 *musculus domesticus*), for instance, have been documented to have an average home range of
226 300m² (Mikesic and Drickamer 1992). When testing the impact of landscape complexity, the
227 central design challenge will be acquiring data at a fine enough resolution. Though certain
228 technologies, such as Light Detection and Ranging (LiDAR), are making sub-meter remote
229 sensing data available, increasingly precise tools will be needed to examine the impact of
230 landscape complexity for species with smaller home ranging requirements. We believe that at
231 these scales future research will further support our findings and possibly identify novel
232 relationships between these smaller species and their complex landscapes.

233 We have demonstrated the importance of landscape complexity for terrestrial home range
234 estimation. We showed that landscape complexity has a significant impact on the measurement
235 of animal home ranges across 18% of the earth's terrestrial surface where vast numbers of
236 animal species are supported. Importantly, the relationship between landscape complexity and
237 animal movement is not limited to home ranging behaviors. We must begin to consider how
238 landscape complexity plays a role in habitat use, resource selection, and animal movement (Heit
239 et al. 2021). By doing so, we can further understand the impact of landscape complexity on
240 animal energetics, inter- and intra-species interactions, and population distributions, amongst
241 others. The incorporation of landscape complexity within existing modeling frameworks will
242 enable researchers to better understand the ecological conditions that correlate with animal

243 movement and ranging requirements. In turn, these new ecological insights can then inform
244 progressive management and conservation practices.

245 **ACKNOWLEDGEMENTS**

246 The authors would like to thank the ASTER database for making their data freely available for
247 the public (<https://doi.org/10.5067/ASTER/ASTGTM.003>). The ASTER GDEM data product
248 used in the preparation of our results were retrieved from the online Data Pool, courtesy of
249 NASA's Earth Observing System Data and Information System (EOSDIS)
250 (<https://earthexplorer.usgs.gov>) We would also like to thank R. Moll for his assistance with
251 the statistical methods of this paper.

252

253 **REFERENCES**

- 254 Adams L (1965) Progress in Ecological Biotelemetry. *Biotelemetry* 15:83–86.
255 <https://doi.org/10.2307/1293341>
- 256 Adams L, Davis SD (1967) The Internal Anatomy of Home Range. *J Mammal* 48:529–536.
257 <https://doi.org/10.2307/1377575>
- 258 Benson E (2010) *Wired Wilderness: Technologies of Tracking and the Making of Modern*
259 *Wildlife*, 1st Edition. Johns Hopkins University Press, Baltimore,MD,USA
- 260 Blair WF (1942) Size of Home Range and Notes on the Life History of the Woodland Deer-
261 Mouse and Eastern Chipmunk in Northern Michigan. *J Mammal* 23:27–36.
262 <https://doi.org/10.2307/1374852>
- 263 Burt WH (1943) Territoriality and Home Range Concepts as Applied to Mammals. *J Mammal*
264 24:346–352. <https://doi.org/10.2307/1374834>
- 265 Cooper C, Larson L, Dayer A, et al (2015) Are Wildlife Recreationists Conservationists?
266 Linking Hunting, Birdwatching, and Pro-Environmental Behavior. *J Wildl Manage* 79:446–
267 457. <https://doi.org/10.1002/jwmg.855>
- 268 Elton CS (1927) *Animal Ecology*. Macmillan Company, New York, USA
- 269 Farhadinia MS, Heit DR, Montgomery RA, et al (2019) Vertical relief facilitates spatial
270 segregation of a high density large carnivore population. *Oikos* 129:346–355.
271 <https://doi.org/10.1111/oik.06724>
- 272 Fleming ACH, Fagan WF, Mueller T, et al (2015) Rigorous home range estimation with
273 movement data : a new autocorrelated kernel density estimator. *Ecology* 96:1182–1188.
274 <https://doi.org/10.1890/14-2010.1>
- 275 Gompper ME, Lesmeister DB, Ray JC, et al (2016) Differential habitat use or intraguild
276 interactions: What structures a carnivore community? *PLoS One* 11:1–18.
277 <https://doi.org/10.1371/journal.pone.0146055>
- 278 Grinnell J (1917) The Niche-Relationships of the California Thrasher. *Auk* 34:427–433
- 279 Hamilton WJJ (1937) Activity and Home Range of the Field Mouse, *Microtus Pennsylvanicus*
280 *Pennsylvanicus*. *Ecology* 18:255–263. <https://doi.org/10.2307/1930464>
- 281 Hansteen TL, Andreassen HP, Ims RA (1997) Effects of Spatiotemporal Scale on
282 Autocorrelation and Home Range Estimators. *J Wildl Manage* 61:280–290
- 283 Haugen AO (1942) Home Range of the Cottontail Rabbit. *Ecology* 23:354–367.
284 <https://doi.org/10.2307/1930675>
- 285 Heit DR, Ortiz-Calo W, Montgomery RA (2021) Landscape complexity persists as a critical
286 source of bias in terrestrial animal home range estimation. *Ecology* 102:.
287 <https://doi.org/10.1002/ecy.3427>
- 288 Hijmans RJ (2020) raster: Geographic Data Analysis and Modeling

- 289 Horne JS, Garton EO, Krone SM, Lewis JS (2007) Analyzing animal movements using
290 Brownian bridges. *Ecology* 88:2354–2363. <https://doi.org/10.1890/06-0957.1>
- 291 Husseman JS, Murray DL, Power G, et al (2003) Assessing differential prey selection patterns
292 between two sympatric large carnivores. *Oikos* 101:591–601.
293 <https://doi.org/10.1034/j.1600-0706.2003.12230.x>
- 294 IUCN Standards and Petitions Committee (2019) Guidelines for Using the IUCN Red List
295 Categories and Criteria. Prepared by the Standards and Petitions Committee
- 296 Jenness JS (2004) Calculating landscape surface area from digital elevation models. *Wildl Soc*
297 *Bull* 32:829–839. [https://doi.org/10.2193/0091-7648\(2004\)032\[0829:clsafd\]2.0.co;2](https://doi.org/10.2193/0091-7648(2004)032[0829:clsafd]2.0.co;2)
- 298 Johnson DH (1980) The Comparison of Usage and Availability Measurements for Evaluating
299 Resource Preference. *Ecology* 61:65–71. <https://doi.org/10.2307/1937156>
- 300 Jones MC, Marron JS, Sheather SJ (1996) A Brief Survey of Bandwidth Selection for Density
301 Estimation. *J Am Stat Assoc* 91:401–407
- 302 Kenward RE (2000) A manual for wildlife radio tagging. Elsevier Science, San Diego, California
- 303 Kie JG, Matthiopoulos J, Fieberg J, et al (2010) The home-range concept: Are traditional
304 estimators still relevant with modern telemetry technology? *Philos Trans R Soc B Biol Sci*
305 365:2221–2231. <https://doi.org/10.1098/rstb.2010.0093>
- 306 Kochanny CO, Delgiudice GD, Fieberg J (2009) Comparing Global Positioning System and
307 Very High Frequency Telemetry Home Ranges of White-Tailed Deer. *J Wildl Manage*
308 73:779–787. <https://doi.org/10.2193/2008-394>
- 309 Kropil R, Smolko P, Garaj P (2015) Home range and migration patterns of male red deer *Cervus*
310 *elaphus* in Western Carpathians. *Eur J Wildl Res* 61:63–72. [https://doi.org/10.1007/s10344-](https://doi.org/10.1007/s10344-014-0874-4)
311 [014-0874-4](https://doi.org/10.1007/s10344-014-0874-4)
- 312 May R, van Dijk J, Wabakken P, et al (2008a) Habitat differentiation within the large-carnivore
313 community of Norway’s multiple-use landscapes. *J Appl Ecol* 45:1382–1391.
314 <https://doi.org/10.1111/j.1365-2664.2008.01527.x>
- 315 May R, Van Dijk J, Wabakken P, et al (2008b) Habitat differentiation within the large-carnivore
316 community of Norway’s multiple-use landscapes. *J Appl Ecol* 45:1382–1391.
317 <https://doi.org/10.1111/j.1365-2664.2008.01527.x>
- 318 Mckinney T, Boe SR, DeVos Jr JC (2016) GIS-based evaluation of escape terrain and desert
319 bighorn sheep populations in Arizona. 31:1229–1236
- 320 Meserve PL (1977) Three-Dimensional Home Ranges of Cricetid Rodents. *J Mammal* 58:549–
321 558. <https://doi.org/10.2307/1380003>
- 322 Mikesic DG, Drickamer LC (1992) Factors Affecting Home-Range Size in House Mice (*Mus*
323 *musculus domesticus*) Living in Outdoor Enclosures. *Am Midl Nat* 127:31.
324 <https://doi.org/10.2307/2426319>
- 325 Montgomery RA, Ortiz-Calo W, Heit DR (2020) Integrating the multi-domainal and multi-
326 dimensional nature of animal movement into ecological modelling. *Ecol Modell*

327 436:109220. <https://doi.org/10.1016/j.ecolmodel.2020.109220>

328 Montgomery RA, Roloff GJ, Ver Hoef JM, Millspaugh JJ (2010) Can We Accurately
329 Characterize Wildlife Resource Use When Telemetry Data Are Imprecise? *J Wildl Manage*
330 74:1917–1925. <https://doi.org/10.2193/2010-019>

331 Nielsen JR, Lundgren B, Kristensen K, Bastardie F (2013) Localisation of Nursery Areas Based
332 on Comparative Analyses of the Horizontal and Vertical Distribution Patterns of Juvenile
333 Baltic Cod (*Gadus morhua*). *PLoS One* 8:. <https://doi.org/10.1371/journal.pone.0070668>

334 Powell RA, Mitchell MS (2012) What is a home range? *J Mammal* 93:948–958.
335 <https://doi.org/10.1644/11-mamm-s-177.1>

336 R Core Team (2020) R: A language and environment for statistical computing.

337 Riley SJ, DeGloria SD, Elliot R (1999) A Terrain Ruggedness Index that Quantifies Topographic
338 Heterogeneity. *Intermt J Sci* 5:23–27. <https://doi.org/citeulike-article-id:8858430>

339 Ripple WJ, Chapron G, López-Bao JV, et al (2016) Saving the World’s Terrestrial Megafauna.
340 *Bioscience* 66:807–812. <https://doi.org/10.1093/biosci/biw092>

341 Sanderson GC (1966) The Study of Mammal Movements: A Review. *J Wildl Manage* 30:215.
342 <https://doi.org/10.2307/3797914>

343 Sappington JM, Longshore KM, Thompson DB (2007) Quantifying Landscape Ruggedness for
344 Animal Habitat Analysis: A Case Study Using Bighorn Sheep in the Mojave Desert. *J Wildl*
345 *Manage* 71:1419–1426. <https://doi.org/10.2193/2005-723>

346 Schoener TW (1981) An empirically based estimate of home range. *Theor Popul Biol* 20:281–
347 325. [https://doi.org/10.1016/0040-5809\(81\)90049-6](https://doi.org/10.1016/0040-5809(81)90049-6)

348 Seaman DE, Millspaugh JJ, Kernohan BJ, et al (1999) Effects of Sample Size on Kernel Home
349 Range Estimates. *J Wildl Manage* 63:739. <https://doi.org/10.2307/3802664>

350 Tomkiewicz SM, Fuller MR, Kie JG, Bates KK (2010) Global positioning system and associated
351 technologies in animal behaviour and ecological research. *Philos Trans R Soc B Biol Sci*
352 365:2163–2176. <https://doi.org/10.1098/rstb.2010.0090>

353 Tracey JA, Sheppard J, Zhu J, et al (2014) Movement-Based estimation and visualization of
354 space use in 3D for wildlife ecology and conservation. *PLoS One* 9:1–15.
355 <https://doi.org/10.1371/journal.pone.0101205>

356 Winkle W Van (1975) Comparison of Several Probabilistic Home-Range Models. *J Wildl*
357 *Manage* 39:118. <https://doi.org/10.2307/3800474>

358 Worton BJ (1987) A review of models of home range for animal movement. *Ecol Modell*
359 38:277–298. [https://doi.org/10.1016/0304-3800\(87\)90101-3](https://doi.org/10.1016/0304-3800(87)90101-3)

360 Zalewski A, Jedrzejewski W, Jedrzejewska B (2004) Mobility and home range use by pine
361 martens (*Martes martes*) in a Polish primeval forest. *Ecoscience* 11:113–122.
362 <https://doi.org/10.1080/11956860.2004.11682815>

363 Zhang Z, Sheppard JK, Swaisgood RR, et al (2014) Ecological scale and seasonal heterogeneity

364 in the spatial behaviors of giant pandas. *Integr Zool* 9:46–60. <https://doi.org/10.1111/1749->
365 4877.12030

366

367 **STATEMENTS AND DECLARATIONS**

368 **Funding**

369 “The authors declare that no funds, grants, or other support were received during the preparation
370 of this manuscript.”

371 **Competing Interests**

372 The authors have no conflicts of interest to declare.

373 **Author Contributions**

374 All authors contributed to ideas, research questions, and designed the methodology; Waldemar
375 Ortiz-Calo collected and analyzed the data; Waldemar Ortiz-Calo, David R. Heit, and Robert A.
376 Montgomery equally contributed to the writing of the final manuscript. All authors contributed
377 critically to the drafts and gave final approval for publication.

378

379 **Table 1.** Summary of the average percent difference and global terrain ruggedness index (TRI)
 380 values for the simulated home range estimates at varying spatial scales indicative of animals with
 381 different body sizes and ranging requirements.

Spatial Scale (km ²)	Number of Samples	Mean Percent Difference	Percent Difference SD	Mean TRI	TRI SD
5 km ²	9,880	2.76	4.82	3.72	3.19
10 km ²	9,849	2.73	4.63	3.68	3.10
100 km ²	9,891	2.85	4.82	3.74	3.15
250 km ²	9,893	2.84	4.68	3.73	3.10

382

383 **Table 2.** Percent distribution of global terrain ruggedness index (TRI) values at varying spatial
 384 scales indicative of animals with different body sizes and ranging requirements.

Spatial Scale (km ²)	Non-Significant (TRI:0-5.23)	Low (TRI:5.23-10)	Medium (TRI:10-15)	High (TRI:15-20)	Extreme (TRI:20+)
5	81.87%	11.73%	4.30%	1.24%	0.87%
10	81.96%	11.86%	4.25%	1.17%	0.76%
100	82.03%	11.93%	4.20%	1.13%	0.71%
250	82.10%	11.99%	4.16%	1.09%	0.66%

385

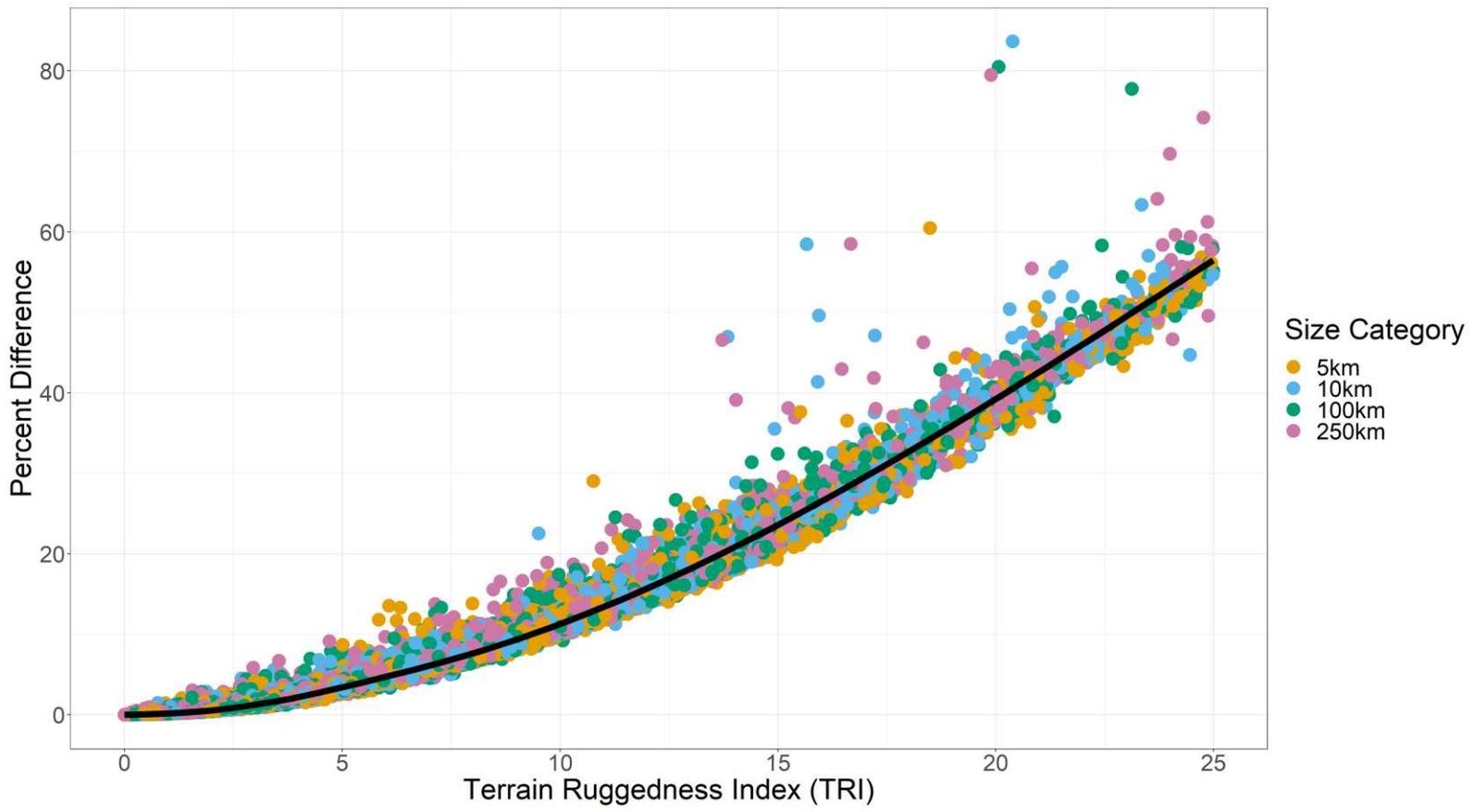
386 **FIGURES LEGEND**

387 **Figure 1.** The quantitative impacts of landscape complexity on traditional (i.e., 2D) home range
388 estimators. These results demonstrate that as landscape complexity increases (as measured by
389 global terrain ruggedness index – TRI), the percent difference between 2D and 2D+ home range
390 estimates expands.

391 **Figure 2.** Global map of landscapes that contain enough complexity to significantly impact the
392 accuracy of home range estimates. An estimated 18% of the earth’s terrestrial landscapes contain
393 enough complexity to statistically bias traditional home range estimates, which are represented in
394 the purple gradient.

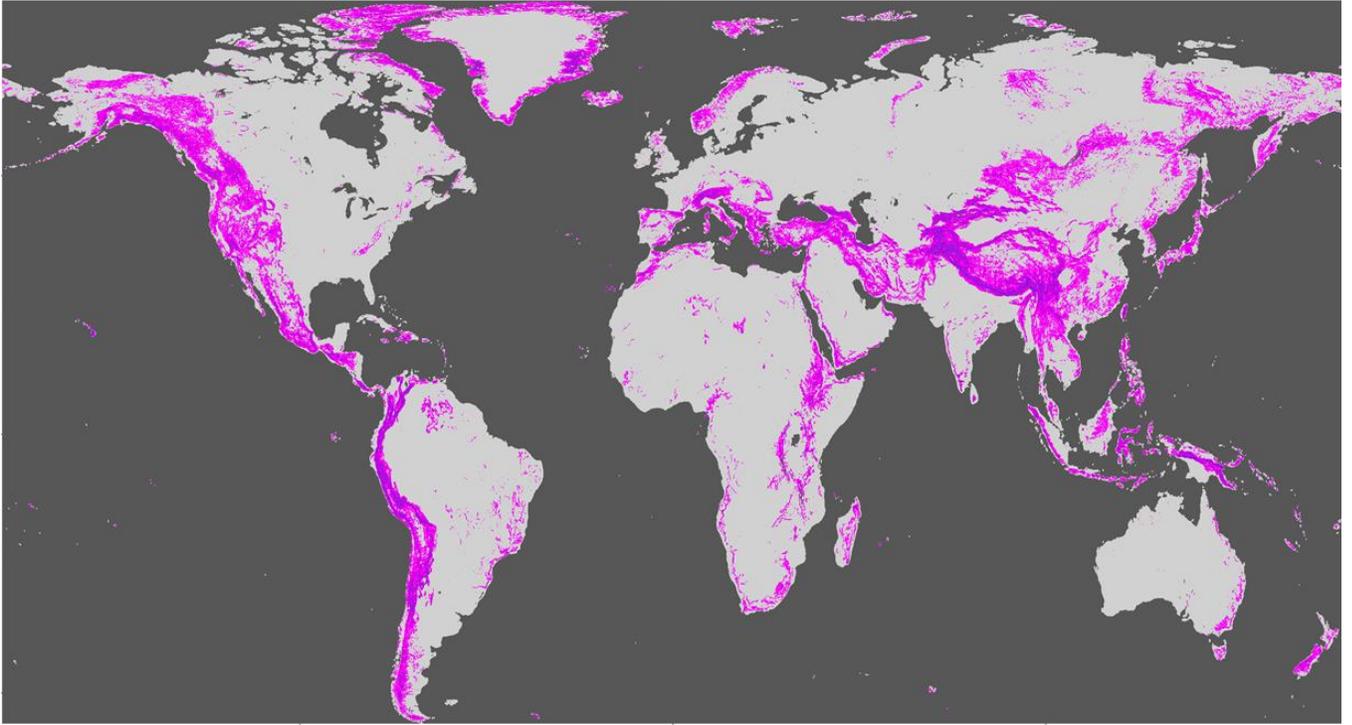
395

396 **Figure 1**



398 **Figure 2**

399



400

401