

Running Head: Animal Home Range Landscape Complexity

Landscape Complexity Persists As a Critical Source of Bias In Terrestrial Animal Home Range Estimation

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AUTHOR CONTRIBUTIONS

All authors have provided equitable contributions to merit authorship on this manuscript. DRH, WOC, and RAM developed the research question and experimental design. DRH, WOC, and RAM contributed to the development of data acquisition methods. DRH facilitated the acquisition of data. DRH analyzed and interpreted the data. DRH, WOC, and RAM contributed the writing and editing of the manuscript. All authors have viewed and approved the current manuscript for publication.

ABSTRACT

Home ranges provide a conceptual and quantitative representation of animal-habitat associations over time. Methods to estimate home ranges have swiftly progressed by dynamically accounting for various sources of bias. Across that period of growth, one potentially influential source of bias has yet to be robustly scrutinized. Animals inhabiting the terrestrial spatial domain make movement decisions in environments with variable landscape complexity. Despite that reality, home range estimation methods tend to be informed by two-dimensional (2D) data (i.e., X and Y coordinates) which analytically presume that these landscapes are flat. This analytical tendency potentially misrepresents the configuration and size of animal home range estimates. To examine the prevalence of this bias, we reviewed literature of terrestrial animal home range estimation published between 2000 and 2019. We recorded the proportion of studies that; *i*) recognized and *ii*) incorporated landscape complexity. Over 22.0% ($n = 271$) of the 1,203 studies recognized the importance of landscape complexity for animal movement. Interestingly, just 0.7% ($n = 8$) incorporated landscape complexity into the home range estimation. We infer then that landscape complexity represents an important source of bias resulting in the underestimation of terrestrial animal home range size. Given the influence of landscape complexity on terrestrial animal decision-making, energetics, and fitness our analysis highlights an important gap in current home range methodologies. We discuss the implications of our analysis for biased understandings of terrestrial animal spatial ecology with subsequent impacts on management and conservation practices built upon these estimates.

Keywords: landscape complexity, fractal dimension, home range estimation, topography, scale, terrestrial wildlife, spatial dimensionality, spatial domainality

INTRODUCTION

Home ranges are a fundamental concept by which animal-habitat relationships are quantified. At the most basic level, animal home ranges represent the post-natal area where an animal satisfies its life history requirements (Burt 1943). Herein, wildlife make decisions to position their home ranges within a broad matrix, informed by landscape characteristics and memory-dependent kinetics (Kie et al. 2005, Gautestad and Mysterud 2006). Though home ranges have historically been estimated using a variety of input data (Montgomery and Roloff 2013), they are most often quantified using animal telemetry (Laver and Kelly 2008, Cagnacci et al. 2010). Since the application of telemetry to ecological research in the mid-20th century, the technology has experienced rapid development and refined resoluteness (Laver and Kelly 2008, Kie et al. 2010, Benson 2010). Coupled with these technological advancements has been tremendous quantitative growth in home range estimation techniques (Kernohan et al. 2001, Cagnacci et al. 2010). Novel approaches have accounted for variable sample sizes (Seaman et al. 1999), bandwidth optimizer (Gitzen et al. 2006), temporal autocorrelation (Fleming et al. 2015), and locational error (Montgomery et al. 2010, 2011). While these factors have been widely referenced in the home range literature, another source of bias represented by spatial dimensionality has yet to be widely scrutinized (Montgomery et al. 2020).

Here, we use the term spatial dimensionality to describe the physical space available for animal movement across all four spatial domains (i.e., aerial, aquatic, subterranean, and terrestrial; Montgomery et al., 2020). This space is comprised of the first, second, and third dimensions, as well as the fractal dimensions in-between. Animals in these domains have

differing ranges of movement resulting from their morphological capabilities (e.g., those that are bound to terra firma). Flying, swimming, and burrowing behavior can theoretically occur in any direction at a given time, while walking in the terrestrial domain will always be bound to some landscape surface (e.g. ground and adjacent vegetation). Consequently, spatial dimensionality in the terrestrial domain tends to consist of topographic or structural complexity (e.g., vegetation, downed timber, and anthropogenic features). Nevertheless, these features present dynamic habitat conditions that often accompany wide-ranging benefits and challenges to animal movement and behavior.

When considering the subsequent analysis of animal movement data in terrestrial landscapes, these sources of complexity in spatial dimensionality can be collectively described as landscape complexity. Terrestrial landscapes, with their undulating topographic surfaces, have features that rise and drop beyond a 2D horizontal plane (Fig. 1). However, full 3D movement is not possible given that terrestrial wildlife are bound to earth via gravity. Thus, terrestrial animal movement is defined by the shape and structure of the landscape surface, which is neither a 2D flat plane nor a 3D volume, but rather is $2D+$ (Fig. 1; Montgomery et al., 2020). Furthermore, the extent of these $2D+$ movements is scale-dependent, varying as a function of animal-habitat interactions (Meager et al. 2011, Bell et al. 2012). Whereas a mountain or boulder may be a barrier to a large-bodied animal, a fallen log or mound of gravel may be equally restrictive to a smaller animal (Stone et al. 1997, Ousterhout and Burkhart 2017, Montgomery et al. 2020). Thus, animals with comparatively smaller body sizes are impeded in their movement by structures and terrain that in no way impede larger animals (Badgley 2010, Bell et al. 2012). The scale of spatial dimensionality, and by extension the grain size of the data used to measure

spatial dimensionality, will determine the amount of landscape complexity that is considered (Mandelbrot 1983, Milne 1997, Jenness 2004).

Thus, there is good reason to believe that spatial dimensionality importantly affects animal movement. Efforts have been made previously to account for spatial dimensionality in the estimation of animal home ranges in the aerial and aquatic spatial domains where 2D+ movement is, perhaps, more obvious (Vivancos et al. 2017, Ferrarini et al. 2018). However, the extent to which comparable developments have occurred among terrestrial home range estimation is not as clear. What is also missing is an appreciation for the consequences of failing to consider landscape complexity in terrestrial animal home range estimation. We hypothesized that in the terrestrial domain, landscape complexity has not yet been widely incorporated into home range estimation. To evaluate this hypothesis, we conducted a review of contemporary home range literature. We discuss the results of our analysis for bias in spatial ecological modelling and the management and conservation policies that have been informed by home range estimates.

METHODS

We examined peer-reviewed literature exploring animal home range estimation in the terrestrial domain. We conducted this review (completed on December 31st, 2019) using the Web of Science Core Collection and structured our search terms as follows: (“wildlife” OR “animal”) AND (“home range” OR “utilization distribution” OR “kernel density estimat*” OR “minimum convex polygon” OR “local convex hull”). We used these terms to search within the title, abstract, and/or keywords of all studies published from 2000 to 2019. This starting point for our review corresponded with the launch of the National Aeronautics and Space Administration (NASA) Shuttle Radar Topography Mission (SRTM) that produced the first publicly-available

global digital elevation models (GDEMs; (Rabus et al. 2003). Given that GDEMs are one of the most widely-used tools to analyze landscape complexity, this temporal extent aligns with the feasibility of incorporating these data into home range estimation (Kamp et al. 2003, Jenness 2004).

Upon examination of all studies, we excluded those that: *i*) featured research subjects in the aerial, aquatic, or subterranean (expressly those capable of burrowing) spatial domains, *ii*) used home range estimates from another primary source, or *iii*) focused on conceptual rather than applied aspects of home range estimation. Among the resultant literature, we assessed the home range estimators used and recorded the various sources of bias that were accounted for including: *i*) bandwidth optimizer (in studies using kernel density estimators), *ii*) sample size, *iii*) locational error, *iv*) temporal autocorrelation, and *v*) spatial dimensionality. With respect to landscape complexity, we documented instances in which the importance of this concept was acknowledged in the study (i.e., landscape complexity was ‘recognized’) and when it was mechanistically incorporated into the home range estimation methods (i.e., ‘incorporated’). For example, studies that *recognized* landscape complexity would be those that commented on topographic or structural movement barriers, used a GDEM for graphical representation, or modeled elevation or slope as a regression covariate. Studies that *incorporated* landscape complexity would be those that fit home range estimation models that accounted for the fractal nature of the landscape. Finally, we examined temporal patterns in both the recognition and incorporation of landscape complexity in terrestrial animal home range estimates.

RESULTS

Our literature review returned 3,219 peer-reviewed studies published between 2000 and 2019. Among this literature, there were 2,016 studies that did not meet our criteria for retention.

In total, 18 different home range estimators were used across these studies (Table 1, Fig. 2). Kernel density estimation (KDE, 54.6%, $n = 657$) and minimum convex polygons (MCP, 51.1%, $n = 614$) were the most common estimators (Table 1). These estimators were often used concurrently and were both used far more often than the next-most-common estimators, the proportions of which ranged from 0.1% and 4.7% of studies (Table 1). We also observed that KDE and MCP have increased in use substantially over time, while the same trends were not experienced for other estimators. A smaller temporal increase was observed for Brownian-bridge movement models, local convex hulls, and autocorrelated KDEs (Fig. 2). Of the 1,203 home range studies that we retained for analysis, 34.3% ($n = 413$) incorporated sample size, 21.4% ($n = 257$) incorporated locational error, and 24.9% ($n = 300$) incorporated temporal autocorrelation (Table 2). Of the 657 KDE studies, 58.8% ($n = 386$) specified a bandwidth optimizer. In comparison, just 0.7% ($n = 8$) of the studies *incorporated* landscape complexity into home range estimation while 22.5% ($n = 271$) *recognized* the importance of this complexity (Table 2). We also observed that while the recognition of landscape complexity and other biases experienced regular increase in prevalence over time, the incorporation of landscape complexity remained consistently low (Fig. 3). Among the eight studies that incorporated landscape complexity in terrestrial home range estimation, the most common method was to extract estimates of surface area from a rasterized GDEM (Table 3).

DISCUSSION

Home ranges have been an essential tool for the study of animal spatial ecology for over 75 years. As a result, numerous inferences about animal ecology are built upon estimates of home range location, size, and configuration. For instance, animal home ranges are used to depict inter and intra-specific interactions (Dillon and Kelly 2008, Deuel et al. 2017), to estimate population density (Trehwella et al. 1988), to evaluate scales of resource selection (Anderson et

al. 2005, Hooten et al. 2013), and as a metric of reproductive success (Mcloughlin et al. 2007), among many others. Thus, the reliability of these measures is dependent on the accuracy of home range estimation. While other sources of bias have been rigorously accounted for in home range estimation, we found that <1% of the studies in our review made efforts to incorporate landscape complexity. This demonstrates that nearly all terrestrial animal home range studies analytically assumed that the surfaces over which animal subjects moved were flat. The comparatively low rates of incorporating spatial dimensionality were evident even though 22.5% ($n = 271$) of the studies formally recognized the importance of landscape complexity. The lack of incorporation of landscape complexity in home range estimation likely represents a considerable source of bias represented by the difference between 2D and 2D+ animal movement.

The severity of this bias undoubtedly depends upon the terrestrial animal and the study area in which that species is studied. Landscape complexity is scale-dependent (Montgomery et al. 2020), but differences between 2D and 2D+ movements are expected to be higher in landscapes with higher complexity (e.g. mountainous habitat). Accordingly, among the finite number of studies that have incorporated landscape complexity, 2D home ranges have been found to underestimate home range size by factors ranging from <1% to 38% (Stone et al. 1997, Campbell et al. 2004, Greenberg and McClintock 2008, Walter et al. 2013, Monterroso et al. 2013, Farhadinia et al. 2019). Of these studies, the higher percentages have been associated with species residing in mountainous habitats (Monterroso et al. 2013, Farhadinia et al. 2019). Mountainous regions across the globe are important refugia for animal biodiversity, and increasingly so due to ongoing global climate change processes (Hoorn et al. 2018). As the climate warms, the species most dependent on very specific climatic and ecological regimes have little choice but to adapt, or to climb. Higher elevations sometimes offer the only suitable habitat

conditions for threatened and endangered species (Maleki Najafabadi et al. 2010, Forrest et al. 2012). Metrics for measuring conservation risk are built, in part, with home range estimates. The International Union for the Conservation of Species (IUCN) uses home range as one of the metrics in determining species extinction risk (IUCN (International Union for Conservation of Nature) 2012). Such decisions are heavily dependent on the data on hand, and inherent to the scarcity of endangered species is the scarcity of such high-quality data (Game et al. 2013). Underestimates nearing 40% clearly represent a significant source of bias that could substantially alter our understanding of animal spatial ecology and subsequently jeopardize the legitimacy of management and conservation practices for these species.

Above and beyond home range sizes, there are several additional conceptual consequences of ignoring landscape complexity. Inferences such as population density and carrying capacity often use 2D measures of separation distance and home range overlap (Stanner and Mendelssohn 1987, Downs et al. 2008). Home ranges are also used as a metric for reproductive and translocation success, with the establishment of a sufficiently sized home range (Fisher and Lara 1999, McLoughlin et al. 2007, Thalmann et al. 2016). These methods overlook potential vertical stratification of animal movement patterns by ignoring vertical relief structures (Davies and Asner 2014, Farhadinia et al. 2019). Areas with broad vertical relief structures could potentially accommodate more individuals by both providing more area for research procurement and by limiting antagonistic inter and intra-specific interaction (Downs et al. 2008, Farhadinia et al. 2019). Similarly, 2D+ landscape features can act as physical barriers to movement beyond solely increasing area. An underlying factor in each of these inferences is that animals may use vertical complexity to avoid inter- and intra-species interactions and use complex landscapes in ways that obscure their true spatial extent from 2D observation. Thus,

spatial analyses that are based upon 2D data have the potential to set up problematic ecological axioms, by presuming accuracy in home range estimation.

Of the studies identified in this review, it is difficult to interpret which study areas present sufficient landscape complexity to present a significant bias. Intuitively, there are areas on the planet, such as areas with flat topography and low land cover heterogeneity, where the impact of landscape complexity may be negligible. Some studies, like Monterosso et al. (2013), have sought to establish a clear threshold for what level of topographic variation significantly impacts home range estimation. However, as previously stated landscape complexity can come from any landscape complexity, not just topography. Currently, the decision of whether and how to address landscape complexity remains largely at the researcher's discretion. We found that most studies that incorporated landscape complexity, did so by obtaining 2D+ surface area from a GDEM. Importantly however, the relationships that can be elucidated between home range size and landscape complexity can be highly impacted by data resolution. While an area may appear to be relatively flat when using a GDEM with a 30-meter resolution, it can predictably increase in complexity when the data are obtained at finer resolution (Wiens 1989). Applications of Light Detection and Ranging (LiDAR) technology is a promising advancement in the study of landscape complexity, with purported resolutions accurate to 10 centimeters (Heidemann 2012). The authors are not aware of existing empirical investigations into whether LiDAR data could account for the fine-scale landscape complexity relevant to incredibly small animals like small rodents and insects. Inference into their relationship with landscape complexity may be beyond the current capabilities of contemporary mapping technologies. This does not mean that 2D+ home ranges are unavailable to studies of smaller-bodied animals. One study we identified in this review estimated the 2D+ home range of pond-breeding salamanders (Ousterhout and Burkhart

2017). These salamanders are bound to existing subterranean tunnels, making their movement a unique hybrid between terrestrial and subterranean. Their small body size makes widely available GDEMs inadequate for estimating a 2D+ home range, so the authors used a 3D kernel volume. Such methods highlight the fact that landscape complexity has implications for animals regardless of scale (see Montgomery et al. 2020).

While only eight studies in our review incorporated landscape complexity, the predominant method used to do so can be readily replicated across species and study sites. For example, computationally-efficient methods to calculate surface area exist in popular geographical and statistical software like ArcGIS and R (Kamp et al. 2003, Rabus et al. 2003, Jenness 2004, Pebesma and Bivand 2005). Such methods add functionality to existing estimators and do not require entirely different methods or a great amount of computing power (see Farhadinia et al. 2019). Thus, incorporating landscape complexity into home range estimation can be accomplished with relative ease, so long as the scale of available GDEMs is relevant to the study species in question. With time and further inquiry, more methods can and should be developed to account for landscape complexity at increasingly smaller scales, and across all spatial domains.

Home ranges are a powerful tool for quantifying animal spatial ecology. We found that the implementation of home range estimation in literature presently overlooks the landscape characteristics that shape animal ranging patterns by considering home ranges only in 2D. The lack of mechanistic incorporation of landscape complexity can lead to the inaccuracy of spatial analyses that utilize home ranges. Thus, we recommend that landscape complexity be approached with a comparable level of rigor to that afforded to other sources of bias in home range estimation including sample size, bandwidth optimizer, temporal autocorrelation, and

locational error. Further research needs to be conducted to determine where, when and with what method landscape complexity could best be accounted for. Landscape complexity should be considered a fundamental component of home ranges, not just for the sake of scientific methodology, but for the sake of animal spatial ecology and conservation across the globe.

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REFERENCES

- Anderson, D. P., M. G. Turner, J. D. Forester, J. Zhu, M. S. Boyce, H. Beyer, and L. Stowell. 2005. Scale-dependent summer resource selection by reintroduced elk in wisconsin, usa. *The Journal of Wildlife Management* 69:298–310.
- Badgley, C. 2010. Tectonics, topography, and mammalian diversity. *Ecography* 33:220–231.
- Bell, S. S., E. D. McCoy, and H. R. Mushinsky. 2012. *Habitat Structure: The physical arrangement of objects in space*. Springer Science & Business Media.
- Benson, E. 2010. *Wired Wilderness: Technologies of Tracking and the Making of Modern Wildlife*. JHU Press.
- Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346–352.
- Cagnacci, F., L. Boitani, R. A. Powell, and M. S. Boyce. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2157–2162.

- 279 Campbell, T. A., B. R. Laseter, W. M. Ford, and K. V. Miller. 2004. Topographic home ranges
280 of white-tailed deer in the central Appalachians. *Southeastern Naturalist* 3:645–652.
- 281 Davies, A. B., and G. P. Asner. 2014. Advances in animal ecology from 3D-LiDAR ecosystem
282 mapping. *Trends in Ecology & Evolution* 29:681–691.
- 283 Deuel, N. R., L. M. Conner, K. V. Miller, M. J. Chamberlain, M. J. Cherry, and L. V.
284 Tannenbaum. 2017. Gray fox home range, spatial overlap, mated pair interactions and
285 extra-territorial forays in southwestern Georgia, USA. *Wildlife Biology:UNSP*
286 *wlb.00326*.
- 287 Dillon, A., and M. J. Kelly. 2008. Ocelot home range, overlap and density: comparing radio
288 telemetry with camera trapping. *Journal of Zoology* 275:391–398.
- 289 Downs, J. A., R. J. Gates, and A. T. Murray. 2008. Estimating carrying capacity for sandhill
290 cranes using habitat suitability and spatial optimization models. *Ecological Modelling*
291 214:284–292.
- 292 Farhadinia, M. S., D. R. Heit, R. A. Montgomery, P. J. Johnson, K. Hobeali, L. T. B. Hunter, and
293 D. W. Macdonald. 2019. Vertical relief facilitates spatial segregation of a high density
294 large carnivore population. *Oikos*.
- 295 Ferrarini, A., G. Giglio, S. C. Pellegrino, A. G. Frassanito, and M. Gustin. 2018. A new
296 methodology for computing birds' 3D home ranges. *Avian Research* 9:19.
- 297 Fisher, D. O., and M. C. Lara. 1999. Effects of body size and home range on access to mates and
298 paternity in male bridled naitail wallabies. *Animal Behaviour* 58:121–130.
- 299 Fleming, C. H., W. F. Fagan, T. Mueller, K. A. Olson, P. Leimgruber, and J. M. Calabrese. 2015.
300 Rigorous home range estimation with movement data: a new autocorrelated kernel
301 density estimator. *Ecology* 96:1182–1188.

- 302 Forrest, J. L., E. Wikramanayake, R. Shrestha, G. Areendran, K. Gyeltshen, A. Maheshwari, S.
 303 Mazumdar, R. Naidoo, G. J. Thapa, and K. Thapa. 2012. Conservation and climate
 304 change: Assessing the vulnerability of snow leopard habitat to treeline shift in the
 305 Himalaya. *Biological Conservation* 150:129–135.
- 306 Game, E. T., P. Kareiva, and H. P. Possingham. 2013. Six Common Mistakes in Conservation
 307 Priority Setting. *Conservation Biology* 27:480–485.
- 308 Gautestad, and L. Mysterud. 2006. Complex animal distribution and abundance from memory-
 309 dependent kinetics. *Ecological Complexity* 3:44–55.
- 310 Gitzen, R. A., J. J. Millspaugh, and B. J. Kernohan. 2006. Bandwidth selection for fixed-kernel
 311 analysis of animal utilization distributions. *Journal of Wildlife Management* 70:1334–
 312 1344.
- 313 Greenberg, D. B., and W. J. McClintock. 2008. Remember the Third Dimension: Terrain
 314 Modeling Improves Estimates of Snake Home Range Size. *Copeia* 2008:801–806.
- 315 Heidemann, H. K. 2012. Lidar metadata:437–470.
- 316 Hoorn, C., A. Perrigo, and A. Antonelli. 2018. *Mountains, Climate and Biodiversity*. John Wiley
 317 & Sons.
- 318 Hooten, M. B., E. M. Hanks, D. S. Johnson, and M. W. Alldredge. 2013. Reconciling resource
 319 utilization and resource selection functions. *Journal of Animal Ecology* 82:1146–1154.
- 320 IUCN (International Union for Conservation of Nature). 2012. IUCN Red List categories and
 321 criteria, version 3.1, second edition. IUCN, Gland, Switzerland.
- 322 Jenness, J. S. 2004. Calculating landscape surface area from digital elevation models. *Wildlife*
 323 *Society Bulletin* 32:829–839.

- 324 Kamp, U., T. Bolch, and J. Olsenholler. 2003. DEM generation from ASTER satellite data for
 325 geomorphometric analysis of Cerro Sillajhuay, Chile/Bolivia. Page 10. Zurich Open
 326 Repository and Archive, University of Zurich, Anchorage, AK, USA.
- 327 Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Chapter 5 - Analysis of Animal Space
 328 Use and Movements. Pages 125–166 *in* J. J. Millspaugh and J. M. Marzluff, editors.
 329 Radio Tracking and Animal Populations. Academic Press, San Diego.
- 330 Kie, J. G., A. A. Ager, and R. T. Bowyer. 2005. Landscape-level movements of North American
 331 elk (*Cervus elaphus*): effects of habitat patch structure and topography. *Landscape*
 332 *Ecology* 20:289–300.
- 333 Kie, J. G., J. Matthiopoulos, J. Fieberg, R. A. Powell, F. Cagnacci, M. S. Mitchell, J.-M.
 334 Gaillard, and P. R. Moorcroft. 2010. The home-range concept: are traditional estimators
 335 still relevant with modern telemetry technology? *Philosophical Transactions of the Royal*
 336 *Society B-Biological Sciences* 365:2221–2231.
- 337 Laver, P. N., and M. J. Kelly. 2008. A Critical Review of Home Range Studies. *The Journal of*
 338 *Wildlife Management* 72:290–298.
- 339 Maleki Najafabadi, S., M. R. Hemami, and A. Salman Mahini. 2010. DETERMINING
 340 HABITAT SUITABILITY OF *OVIS ORIENTALIS ISFAHANICA* IN MOTHE
 341 WILDLIFE REFUGE USING ENFA 63:279–290.
- 342 Mandelbrot, B. 1983. *The fractal geometry of nature*. WH freeman New York.
- 343 Mcloughlin, P. D., J.-M. Gaillard, M. S. Boyce, C. Bonenfant, F. Messier, P. Duncan, D.
 344 Delorme, B. Van Moorter, S. Said, and F. Klein. 2007. Lifetime reproductive success and
 345 composition of the home range in a large herbivore. *Ecology* 88:3192–3201.

- 346 Meager, J. J., T. A. Schlacher, and M. Green. 2011. Topographic complexity and landscape
347 temperature patterns create a dynamic habitat structure on a rocky intertidal shore.
348 *Marine Ecology Progress Series* 428:1–12.
- 349 Milne, B. T. 1997. Applications of Fractal Geometry in Wildlife Biology. *Wildlife and*
350 *Landscape Ecology*:32–69.
- 351 Monterroso, P., N. Sillero, L. M. Rosalino, F. Loureiro, and P. C. Alves. 2013. Estimating home-
352 range size: when to include a third dimension? *Ecology and Evolution* 3:2285–2295.
- 353 Montgomery, R. A., D. R. Heit, and W. Ortiz-Calo. 2020. Integrating the multi-domainal and
354 multi-dimensional nature of animal movement into ecological modelling. *Ecological*
355 *Modelling* 436.
- 356 Montgomery, R. A., and G. J. Roloff. 2013. Habitat Selection. Pages 59–69 *in* S. A. Levin,
357 editor. *Encyclopedia of Biodiversity* (Second Edition). Academic Press, Waltham.
- 358 Montgomery, R. A., G. J. Roloff, and J. M. V. Hoef. 2011. Implications of ignoring telemetry
359 error on inference in wildlife resource use models. *The Journal of Wildlife Management*
360 75:702–708.
- 361 Montgomery, R. A., G. J. Roloff, J. M. V. Hoef, and J. J. Millspaugh. 2010. Can we accurately
362 characterize wildlife resource use when telemetry data are imprecise? *Journal of Wildlife*
363 *Management* 74:1917–1925.
- 364 Ousterhout, B. H., and J. J. Burkhart. 2017. Moving beyond the plane: measuring 3D home
365 ranges of juvenile salamanders with passive integrated transponder (PIT) tags. *Behavioral*
366 *Ecology and Sociobiology* 71:1–15.
- 367 Pebesma, E., and R. S. Bivand. 2005. *Classes and Methods for Spatial Data: the sp Package*:21.

- 368 Rabus, B., M. Eineder, A. Roth, and R. Bamler. 2003. The shuttle radar topography mission—a
369 new class of digital elevation models acquired by spaceborne radar. *ISPRS Journal of*
370 *Photogrammetry and Remote Sensing* 57:241–262.
- 371 Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A.
372 Gitzen. 1999. Effects of Sample Size on Kernel Home Range Estimates. *The Journal of*
373 *Wildlife Management* 63:739–747.
- 374 Stanner, M., and H. Mendelssohn. 1987. Sex Ratio, Population Density and Home Range of the
375 Desert Monitor (*Varanus griseus*) in the Southern Coastal Plain of Israel. *Amphibia-*
376 *Reptilia* 8:153–163.
- 377 Stone, K. D., G. A. Heidt, P. T. Caster, and M. L. Kennedy. 1997. Using geographic information
378 systems to determine home range of the southern flying squirrel (*Glaucomys volans*). *The*
379 *American Midland Naturalist* 137:106-.
- 380 Thalmann, S., S. Peck, P. Wise, J. M. Potts, J. Clarke, and J. Richley. 2016. Translocation of a
381 top-order carnivore: tracking the initial survival, spatial movement, home-range
382 establishment and habitat use of Tasmanian devils on Maria Island. *Australian*
383 *Mammalogy* 38:68–79.
- 384 Trehwella, W. J., S. Harris, and F. E. McAllister. 1988. Dispersal Distance, Home-Range Size
385 and Population Density in the Red Fox (*Vulpes vulpes*): A Quantitative Analysis. *Journal*
386 *of Applied Ecology* 25:423–434.
- 387 Vivancos, A., G. Closs, and C. Tentelier. 2017. Are 2D space-use analyses adapted to animals
388 living in 3D environments? A case study on a fish shoal. *Behavioral Ecology* 28:485–
389 493.

- Walter, W. D., J. W. Fischer, T. J. Fink, S. E. Hygnstrom, J. A. Jenks, and K. C. Vercauteren.
2013. Topographic Home Range of Large Mammals: Is Planimetric Home Range Still a
Viable Method? *The Prairie Naturalist*:9.
- Wiens, J. A. 1989. Spatial Scaling in Ecology. *Functional Ecology* 3:385–397.

413 **TABLES**

414 **Table 1.** The home range estimators used in studies obtained via a review of terrestrial home
 415 range literature published between 2000 and 2019. Proportions (given in percentages) are of the
 416 studies retained for analysis ($n = 1,203$). Proportion of studies that used identified kernel
 417 bandwidth optimizers were only taken out of the number of studies that used kernel density
 418 estimation as their home range estimator.

Home Range Estimators	# Studies	% of Total
Studies in initial search	3,219	-
Studies retained for analysis (Total)	1,203	-
Home range estimator used		
Kernel Density Estimation (KDE)	657	54.6
Specified bandwidth optimizer	386	58.8
Minimum Convex Polygon (MCP)	614	51.1
KDE and MCP concurrently	247	20.5
Brownian-Bridge Movement	56	4.65
Local Convex Hull	52	4.32
Harmonic Mean	24	1.99
Manual/Analog	13	1.08
Unknown/Unnamed	13	1.08
Autocorrelated KDE	11	0.91
Movement KDE	10	0.83
Bivariate Normal Ellipse	6	0.49
K Cluster	4	0.33
Biased Random Bridge	3	0.24
Characteristic Hull Polygon	2	0.16
Continuous-Time Movement Model	1	0.08
Individual-based Ectotherm Movement	1	0.08
Concave Polygon	1	0.08
Bound Strip	1	0.08
Nearest-neighbor Voronoi Distribution	1	0.08

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Table 2. Sources of bias addressed in studies obtained via a review of terrestrial home range literature published between 2000 and 2019. Proportions (given in percentages) are of the studies retained for analysis ($n = 1,203$). Studies that addressed landscape complexity were divided into two groups, those that recognized, in writing, the impact of landscape complexity and those that incorporated it directly into their methods.

Sources of Bias	# Studies	% of Total
Studies in initial search	3,219	-
Studies retained for analysis (Total)	1,203	-
Biases Recognized and Incorporated		
Recognized Landscape Complexity	271	22.5
Incorporated Landscape Complexity	8	0.67
Inc. Sample Size	413	34.3
Inc. Temporal Autocorrelation	300	24.9
Inc. Telemetry Error	257	21.3

Table 3. Analysis of methods used and biases accounted for in home range studies obtained via review of terrestrial home range literature published between 2000 and 2019. Of studies retained for analysis ($n = 1,203$), studies in the table were determined to have properly incorporated spatial dimensionality in their methods ($n = 11$). The biases evaluated were: telemetry error, kernel bandwidth optimizer, temporal autocorrelation, and sample size. Methods to account for 2D+ animal movement and landscape features were: calculating surface area from a global digital elevation model (GDEM surf. area), and in one case the authors used a 3D kernel volume. Home range estimators used were kernel density estimation (KDE), minimum convex polygon (MCP), autocorrelated KDE (AKDE), movement KDE (MKDE).

<i>Title</i>			
Authors	Year	2D+ Method	Estimator
<i>The spatial patterns of Alpine chamois (<i>Rupicapra rupicapra rupicapra</i>) and their influence on population dynamics in the Swiss National Park</i>			
Boschi & Nievergelt	2003	GDEM surf. area	KDE
<i>Topographic home ranges of white-tailed deer in the central Appalachians</i>			
Campbell <i>et al.</i>	2004	GDEM surf. area	KDE
<i>Vertical relief facilitates spatial segregation of a high density large carnivore population</i>			
Farhadinia <i>et al.</i>	2019	GDEM surf. area	AKDE
<i>Remember the third dimension: terrain modeling improves estimates of snake home range size</i>			
Greenberg & McClintock	2008	GDEM surf. area	MCP
<i>Estimating home-range size: when to include a third dimension?</i>			
Monterroso <i>et al.</i>	2013	GDEM surf. area	MCP
<i>Moving beyond the plane: measuring 3D home ranges of juvenile salamanders with passive integrated transponder (PIT) tags</i>			
Ousterhout & Burkhart	2017	3D kernel volume	KDE
<i>From steps to home range formation: species-specific movement upscaling among sympatric ungulates</i>			
Tablado <i>et al.</i>	2016	GDEM surf. area	MCP
<i>Movement-based estimation and visualization of space use in 3D for wildlife ecology and conservation</i>			
Tracey <i>et al.</i>	2014	GDEM surf. area	MKDE

FIGURE CAPTIONS

Figure 1. Home ranges are typically informed by two-dimensional (i.e., X and Y coordinates) input data where the resultant estimate is typically a flat polygon (panel a). This conceptualization inherently assumes that landscapes are flat, when that is rarely the case in nature (panel b). Terrestrial animals traverse landscapes with varying amounts of landscape complexity (panel c). Therefore, terrestrial home ranges would be more accurately depicted as surfaces that incorporate this landscape complexity into a $2D+$ home range estimate (panel d). Such home ranges would have comparatively higher surface areas than those estimated in 2D.

Figure 2. The 10 most common home range estimators used per year in studies retained for analysis ($n = 1,203$) in a review of terrestrial home range literature published between the 2000 and 2019. Estimators include: kernel density estimation (KDE), minimum convex polygon (MCP), Brownian-bridge Movement Model (BBMM), autocorrelated KDE (AKDE), movement KDE (MKDE), local convex hull (LOCOH), harmonic mean (HARMONIC), k-cluster (KCLUSTER), analog/manual (MANUAL).

Figure 3. Sources of bias addressed per year in studies retained for analysis ($n = 1,203$) in a review of terrestrial home range literature published between the 2000 and 2019. Trends in this figure from studies relating to landscape complexity are of those that incorporated it directly into their methods (Inc), and those that recognized its importance (Rec).