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Topographic Home Range of Large Mammals: Is Planimetric Home Range Still a Viable Method?

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ABSTRACT Topography influences movement trajectories, quality of forages used, and behavioral response of large herbivores to anthropogenic disturbances, but research is lacking on the influence of terrain complexity on size of home range. Size of home range usually is based on planimetric area and therefore rarely accounts for the true surface area traversed by an animal. We conducted radiotelemetry on bighorn sheep (*Ovis canadensis*), Rocky Mountain elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*) equipped with VHF collars at three sites from 2002 to 2006 to document size of home range in areas that ranged from 400 m to 1,500 m in elevation with varying degrees of topographic ruggedness in the Great Plains. We used the fixed-kernel method to compare size of 95% home range between two-dimensional (planimetric) and three-dimensional (topographic) estimates. Mean (± SD) percent increase in size of home range from planimetric to topographic was 2.8% (± 0.19), 1.2 % (± 0.52), 1.0% (± 0.43), and 0.1% (± 0.40) for bighorn sheep, elk, mule deer, and white-tailed deer, respectively. We found little difference in size between planimetric and topographic home range for our species suggesting that planimetric home range techniques are likely valid in the Great Plains and similar regions but both home range methods should be compared in other regions with high topographic relief (e.g., Rocky Mountain region).

KEY WORDS home range, *Odocoileus* spp., *Ovis canadensis*, planimetric, radiotelemetry, topographic.

Home range is considered the extent of area with a defined probability of occurrence of an animal during a specified period (Kernohan et al. 2001). Home range estimators have evolved over the past several decades from simplistic minimum convex polygons that encompass the perimeter of an animal's range (Mohr 1947) to kernel estimation that results in a utilization distribution of probability of occurrence in an area (Worton 1989). All home range estimators calculate area of home range based on a two-dimensional plane (planimetric), but do not account for gradients in elevation or ruggedness of a landscape. Jenness (2004) quantified the variability of topography within and between study areas by calculating landscape surface area from Digital Elevation Models (DEM). Researchers have used surface area to estimate size of home range in three-dimensions (topographic) in comparisons to planimetric home range. For example, size of planimetric home range increased 3.1%, 6.4%, and 8.5% after incorporating topography for white-tailed deer (*Odocoileus virginianus*), Alleghany woodrats (*Neotoma magister*), and southern flying squirrel (*Glaucomys volans*), respectively (Stone et al. 1997, Castleberry et al. 2001, Campbell et al. 2004).

With advances in Geographic Information Systems (GIS) and wide-scale availability of regional data, comparison of size of home range within species across landscapes is common (Kie et al. 2002, Anderson et al. 2005, Walter et al. 2009). Estimates of size of home range were compared across populations of Rocky Mountain elk (*Cervus elaphus*) in Wisconsin, Alberta, and Wyoming with elevations ranging from 500 m to >2,400 m of varying topographical relief (Anderson et al. 2005). Size of home range for mule deer (*O. hemionus*) that occupied elevations that ranged from 475 m to 3,500 m were compared across five diverse sites throughout California (Kie et al. 2002). Elevation ranged from 115 m to 302 m in comparisons of size of home range for white-tailed deer across four states in the agricultural Midwest with minimal variation in topographic relief (Walter et al. 2009). Even with topographical layers that are freely-available for GIS applications, none of the aforementioned studies considered variation in topography among regions on estimates of size of home range.

Only one study has compared methods of home range in three-dimensional space within or among large mammals and this study was on a single species (Campbell et al. 2004). To our knowledge, no study has assessed home range across a geographic region or with geographic variables (e.g., elevation, surface ruggedness) that may influence estimates of home range in three-dimensional space. As methods of esti-

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mation of home range have evolved along with GIS capabilities (i.e., kernel and movement-based estimators; Walter et al. 2011*b*), so to should estimators that incorporate three-dimensional landforms that influence movements and energetics (Parker et al. 1984, Kie et al. 2005). We investigated measures of topographic home range compared to planimetric home range in bighorn sheep, elk, mule deer, and white-tailed deer to determine if there would be an expected increase in size of home range from planimetric to topographic over a range of landscapes.

METHODS

Study sites

We conducted our study of bighorn sheep (*Ovis canadensis)* in Badlands National Park (BNP) located in Pennington, Shannon, and Jackson counties within the White River badlands of southwestern South Dakota (Fig. 1; Zimmerman 2008). Sharp gradients in elevation (700 to 1,000 m) occur throughout the region (Table 1; Sweanor et al. 1995). Topography of the badlands was formed because of the coincidence of elevation, rainfall, carving action of streams and substrate, resulting in slumps, natural bridges, arches, sod tables, toadstools, and isolated flat remnants of the higher plains (Weedon 1999).

We conducted our study on Rocky Mountain elk within the Wichita Mountains Wildlife Refuge (WMWR) in southwestern Oklahoma, that encompassed Caddo, Comanche, and Kiowa Counties and private lands north of WMWR (Fig. 1; Walter et al. 2005). Igneous mountain peaks with slopes >25° (Hoffman 1930) typified the northern part of WMWR and extended northward into private land, referred to as the Granite Area, with 25% forest cover in a mosaic of native warm sea-

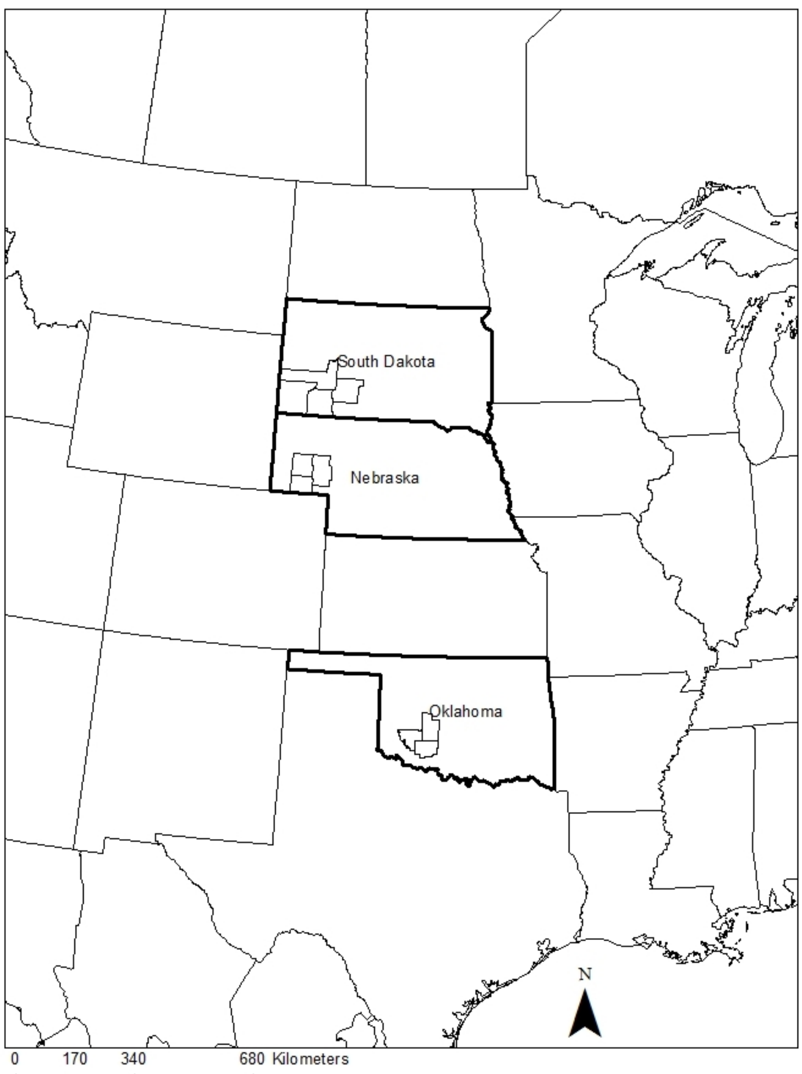

Figure 1. Locations of counties for estimates of home range for bighorn sheep (*Ovis canadensis*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*) in three study areas in the Great Plains, 2002–2006.

son grasses. Limestone-derived rolling hills, referred to as the Slick Hills, occurred three to five km north of WMWR, and adjacent to the northern extent of the Granite Area on private land. The mountains of WMWR and the Granite Area vary in topography from gentle slopes with a minimum elevation of 390 m to the highest elevation in the west at 750 m with the limestone-derived rolling hills ranging in elevation from 444 to 645 m (Table 1).

We conducted our study on mule deer and white-tailed deer in the North Platte River Valley, Nebraska that included Cheyenne, Garden, and Morrill counties (Fig. 1; Walter et al. 2011*a*). Morrill County, where most deer activity occurred, was composed of three distinct regions of mixed hardwood forest, Sandhills, and short-grass prairie. Most of the irrigated crops were grown within three km of the North Platte River. The northern portions of Morrill County were located in the Sandhills, grass-stabilized aeolian sand dunes that contained a variety of native plant communities ranging from upland prairie to wetlands. The southern portion of Morrill County was dominated by short-grass prairie of varying topography and agricultural fields with a range in elevation for the entire study region from 1,094 to 1,325 m (Table 1).

Capture and radiotelemetry

Bighorn sheep.—In September 2004 personnel at BNP, the South Dakota Department of Game, Fish and Parks, and the New Mexico Department of Game and Fish, captured, radiocollared, and relocated Rocky Mountain bighorn sheep from Wheeler Peak in north-central, New Mexico to BNP (Table 1; Zimmerman 2008). We visually relocated 15 radiocollared females from September 2004 to 2006 using handheld and omni-directional antennas and identified all individuals within the group by radiocollar color, ear tag, or distinguishable markings (Zimmerman 2008). We calculated Universal Transverse Mercator (UTM) position of the individual or group based on the location of the observer collected with a handheld GPS, distance to the animal using a Leica© 1200

Table 1. A summary of capture methods, radiocollars, and radiotelemetry sampling designs for the three study areas included in planimetric and topographic estimates of home range of bighorn sheep, Rocky Mountain elk, mule deer (MD), and white-tailed deer (WT) in the Great Plains, 2002–2006.

Variables	Bighorn Sheep	Elk	Deer
Study area size (km^2)	984	238	3,703
Elevation range (m)	700–1,000	390–750	1,094–1,325
Mean annual precipitation (cm)	41	82	42
Mean temperature range (° C)	−41 to 47	3 to 29	−9 to 33
Capture method[a]	CI, DN	CI, HNG	CI, NC, HNG
Collar type (*n*)	VHF (15)	VHF (21)	VHF (19 MD, 27 WT)
Manufacturer[b]	ATS	ATS	ATS
Triangulation technique[c]	Visual	FHH	FVM, MTS
Monitoring	≥3/week	≥4/month	≥3/week
Number of locations	3,782	2,657	5,150 (MD) 4,580 (WT)
Location collection times	diurnal	24-hr	24-hr
Mean duration (1st to final reading)	NA	<30 min	<10 min
Error ellipse (ha)	NA	30	≤10
Error distance (m)	NA	183	123
Angle error	NA	±11°	±1.89°
Kernel estimator	Fixed	Fixed	Fixed
Triangulation program[d]	NA	LOCATE	LOAS
Protocol[e]	ASM, IACUC	IACUC-GU-02-01	IACUC-99-03-014

[a] CI = chemical immobilization, DN = drop net, NC = netted-cage traps, HNG = helicopter net gunning; [b] ATS = Advanced Telemetry Systems, Inc., Isanti, MN, USA; [c] FHH = Fixed, hand-held, FVM = Fixed, vehicle-mounted, MTS = mobile-tracking system; [d] NA = Not applicable; LOCATE = Pacer Computer Software, Truro, Nova Scotia, Canada; LOAS = Location of a Signal, Ecological Software Solutions LLC, Urnäsch, Switzerland; [e] IACUC = Institutional Animal Care and Use Committee Permit, ASM = Guidelines followed by the American Society of Mammalogist

rangefinder (Leica Camera AG, Solms, Germany) accurate to ± 1 m, azimuth using a compass, and the vertical angle of the line of sight using a clinometer.

Rocky Mountain elk.—We recorded locations for 21 adult (i.e., ≥2.5 years-of-age), free-ranging female elk on private lands from April 2002 to March 2005 that were fitted with radiocollars (Table 1). We recorded additional locations of elk groups during random nocturnal bimonthly vehicular excursions throughout the study area using a spotlight, efforts to chemically immobilize elk at bait sites, autumn aerial surveys, ground-based "homing" on radio signals until the radiocollared elk was observed (White and Garrott 1990), and random traverses of the study area on foot to collect fecal samples (Walter et al. 2010).

Mule deer and white-tailed deer.—We monitored 46 free-ranging male and female deer that included 19 mule deer (7 male, 12 female) and 27 white-tailed deer (13 male, 14 female) from March 2004 to September 2007 and equipped deer with individualized ear tags and radiocollars (Table 1). We used aerial telemetry on four occasions to locate deer that dispersed or migrated. For each location, we collected 2−4 bearings consecutively using triangulation and biangulation (White and Garrott 1990). Random observations of marked deer during field work were digitized on-site using Geographic Information Systems (GIS) software ArcView 3.2 (ArcView; Environmental System Research Institute, Redlands, CA, USA) and a 1:24,000 scale United States Geological Survey digital aerial photo. We found no difference in size of planimetric home range by sex for either species of deer so sexes were combined in all subsequent analysis (mule deer, $P = 0.219$; white-tailed deer, $P = 0.078$; Walter et al. 2011*a*).

Planimetric home range

The median number of locations used to calculate home ranges was 277, 103, 364, and 118 for bighorn sheep, elk, mule deer, and white-tailed deer, respectively. We calculated two-dimensional 95% fixed-kernel estimates of size of home range (hereafter referred to as planimetric home range) from vector polygons for all locations of an individual animal (Worton 1989, Seaman and Powell 1996, Seaman et al. 1999). We determined the amount of smoothing by the least-squares cross-validation (h_{lscv}) method with the default parameter in the Home Range Extension of ArcView 3.2 (ArcView; Worton 1989, Rodgers and Carr 1998).

Topographic home range

We calculated the three-dimensional surface area in ArcMap 9.2 (ArcMap; Environmental Systems Research Institute) using standard 30-m United States Geological Survey DEMs and the DEM Surface Tools for ArcMap extension (Jenness 2011). We acquired all DEM data from United States Department of Agriculture, Natural Resource Conservation Service (http://datagateway.nrcs.usda.gov/). We used the surface area tool to calculate true surface area of the landscape for each grid cell using the DEM elevation from the surrounding eight cells. The new grid cell values represented the three-dimensional surface area for the land area contained within that cell's boundaries. We then summed all grid cell values within the animal's vector home-range polygon to derive a topographic home range for each individual. Only raster cells with centers located within a home range vector polygon were summed to calculate the three-dimensional surface area. The accuracy of surface-area calculations derived from raster-based methods tend to produce better results at cell counts >250 so topographic home range cell counts for all species included in this study were >250 (Jenness 2004).

All estimates of home range were calculated for all locations collected for each individual for the duration of the study, thus no seasonal or annual home ranges were calculated to prevent pseudoreplication. Due to multiple species and data collection protocols used in this analysis, comparisons across seasons or years may have provided additional information but our primary objective was to determine differences in estimates of planimetric and topographic home range in the Great Plains. We compared differences within each of four species using a paired t-test and set statistical significance at $P = 0.05$. We performed statistical analysis using Program R (R Development Core Team 2009).

RESULTS

Mean (±SD) size of planimetric home range was 16.2 km^2 (± 5.0), 48.8 km^2 (± 26.5), 16.2 km^2 (± 13.5), and 8.0 km^2 (± 7.1) for bighorn sheep, elk, mule deer, and white-tailed deer, respectively. Mean (±SD) size of topographic home range was 16.6 km^2 (± 5.1), 49.3 km^2 (± 26.6), 16.3 km^2 (± 13.6), and 8.0 km^2 (± 7.1) for bighorn sheep, elk, mule deer, and white-tailed deer, respectively. Mean (±SD) absolute difference in size of planimetric and topographic home range varied from a low of no difference in a white-tailed deer to 91 km^2 in an elk. Mean (±SD) percent increase in size of home range from planimetric to topographic estimates was 2.77% (± 0.19), 1.16 % (± 0.52), 0.98% (± 0.43), and 0.11% (± 0.40) for bighorn sheep, elk, mule deer, and white-tailed deer, respectively. Size of planimetric and topographic home range differed for bighorn sheep ($t_{14} = 12.65$, $P < 0.001$), elk ($t_{20} = 11.28$, $P < 0.001$), and mule deer ($t_{18} = 5.85$, $P = 0.015$) but not for white-tailed deer ($t_{26} = 1.42$, $P = 0.169$).

DISCUSSION

Size of topographic home range compared to planimetric home range increased for three of the four species across geographic regions of the Great Plains. Although elevation across our study sites only ranged from 444 to 1,325 m, the greatest difference in size of home range was for bighorn sheep (Fig.

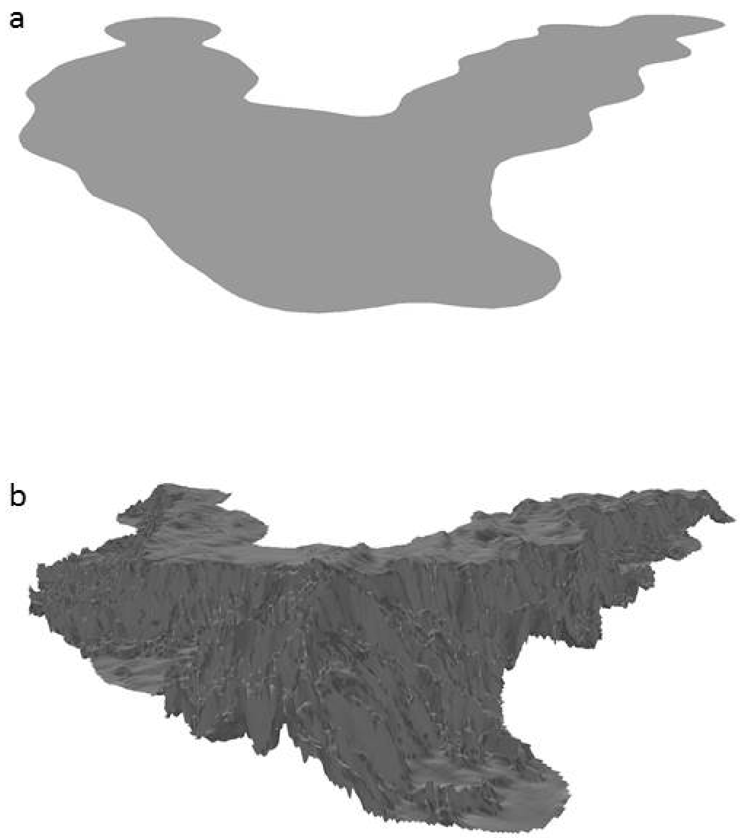

Figure 2. Depiction of a) two-dimensional planimetric and b) three-dimensional topographic home range polygon for a bighorn sheep (*Ovis canadensis*) in western South Dakota, USA.

2). Bighorn sheep occupied Badlands National Park, which was characterized by minimal elevation change (~300 m) but had badland formations of steep cliffs with slopes up to 71°. Difference between planimetric and topographic home range of bighorn sheep would be expected when compared to white-tailed deer that occupied relatively flat riparian areas in western Nebraska with slopes <25°. Elk in Oklahoma occupied mountainous terrain with slopes exceeding 25° with percent difference between topographic and planimetric size of home range being intermediate between bighorn sheep and deer. Although elevation varied more and slopes were >25° in some areas occupied by elk, most were not traversable as they were dominated by large talus boulders and high jagged peaks of bare rock (Hoffman 1930). Collectively, several components of topographical relief (e.g., elevation, ruggedness) should be explored prior to determining type of home range used (e.g., topographic, planimetric) to compare across species or regions.

Energy expenditures and movements vary seasonally for some ungulates in North America that occupy areas that vary in elevation, slope, and topographic ruggedness (Dailey and Hobbs 1989, Kie et al. 2005, Sappington et al. 2007) indicating the potential importance of incorporating topographic variables into analysis of home range in areas with considerable variability in topographic relief. Dailey and Hobbs (1989) demonstrated that energy expenditures increased for bighorn sheep when angle of ascension increased about 20° indicating that slope has considerable influence on area and selection of topography within an animal's home range. Furthermore, species associated with geographic features on the landscape (e.g., rivers, valleys) tend to have linear home-ranges that follow these features (Maier et al. 1998, Kie et al. 2005). Therefore, energetic costs of locomotion in steep terrain may be an important factor contributing to seasonal distribution and abundance of ungulates that should be explored with topographic home range.

Although our differences in planimetric compared to topographic home range were minimal and varied by species, an examination of how well a species' home range can be described by the planimetric area, and when it would be more appropriate to use topographic area or related biological concepts is possible with today's technology. Use of topographic over planimetric home range could be explored in regions containing large mammals that migrate seasonally or in landscapes with greater topographical relief than our study sites. Seasonal variation may identify more pronounced differences in size of home range within and among ungulate species or for carnivores that cover large territories (e.g., wolves [*Canis* *lupis*], mountain lions [*Puma concolor*]). Ungulates typically not associated with steep terrain (e.g., elk, deer) often occupy low-elevation winter ranges (i.e., elevation change <400 m) followed by migrations to higher elevations in response to plant phenology with elevation changes of up to 3,000 m between resident and migratory ranges (Lubow et al. 2002, Post et al. 2003, Conner and Miller 2004). Topographic home range could be explored in comparisons of size of home range between individuals that are year-round residents at low elevations, such as with migratory mule deer in western Nebraska (Walter et al. 2011*a*), to migrants traveling between low and high elevations seasonally such as mule deer and elk in the Rocky Mountain region (Kie et al. 2002, Conner and Miller 2004).

MANAGEMENT IMPLICATIONS

Based on the minimal differences we found in the Great Plains of North America which encompasses limited topographical differences across a species' range (e.g., elevation change >400 m), use of planimetric home range appears to be suitable in areas with minimal topographic differences. Methods to identify additional characteristics in topographically diverse areas, however, could be explored further to expand the concept of home range in studies on movement, home range, and resource selection of large mammals (Fieberg and Börger 2012). For example, with GPS datasets collecting locations in near real-time, the energetics of traversing "non-flat" areas into a home range could be explored using step-by-step movement vectors (Kie et al. 2005) and previous data on energetic expenditures (Dailey and Hobbs 1989). Furthermore, an assessment of selecting for or against areas with steep terrain or if animals that have more rugged terrain in their home range also have higher/lower fitness (e.g., better survival/reproductive rates) could also be explored within the concepts of economic and mechanistic models of home range (Mitchell and Powell 2012, Moorcroft 2012). Our limited data provided by VHF locations prevented such detailed analyses but studies designed with GPS technology in topographically diverse study areas may be able to contribute to these concepts.

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