

## Evaluating distributional shifts in home range estimates

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## Introduction

Location data are often used to estimate animal space use to delineate the predicted area of occurrence for individuals or groups of animals. Traditional methods of estimating home ranges are as simple as a minimum convex polygon (MCP), where peripheral animal locations are connected to create a single polygon with no concave elements (Blair 1940; Mohr 1947). Modern global positioning system (GPS) technologies increase the ability to gather and store voluminous location data with high accuracy in comparison with very high frequency (VHF) systems (Tomkiewicz et al. 2010; Walter et al. 2011; Moorcroft 2012) that cannot utilize satellite technology or store location data. Accordingly, home range estimators have evolved to quantify home ranges using high-volume GPS data and often provide estimates of the intensity of

## Abstract

A variety of methods are commonly used to quantify animal home ranges using location data acquired with telemetry. High-volume location data from global positioning system (GPS) technology provide researchers the opportunity to identify various intensities of use within home ranges, typically quantified through utilization distributions (UDs). However, the wide range of variability evident within UD's constructed with modern home range estimators is often overlooked or ignored during home range comparisons, and challenges may arise when summarizing distributional shifts among multiple UD's. We describe an approach to gain additional insight into home range changes by comparing UD's across isopleths and summarizing comparisons into meaningful results. To demonstrate the efficacy of this approach, we used GPS location data from 16 bighorn sheep (*Ovis canadensis*) to identify distributional changes before and after habitat alterations, and we discuss advantages in its application when comparing home range size, overlap, and joint-space use. We found a consistent increase in bighorn sheep home range size when measured across home range levels, but that home range overlap and similarity values decreased when examined at increasing core levels. Our results highlight the benefit of conducting multiscale assessments when comparing distributions, and we encourage researchers to expand comparative home range analyses to gain a more comprehensive evaluation of distributional changes and to evaluate comparisons across home range levels.

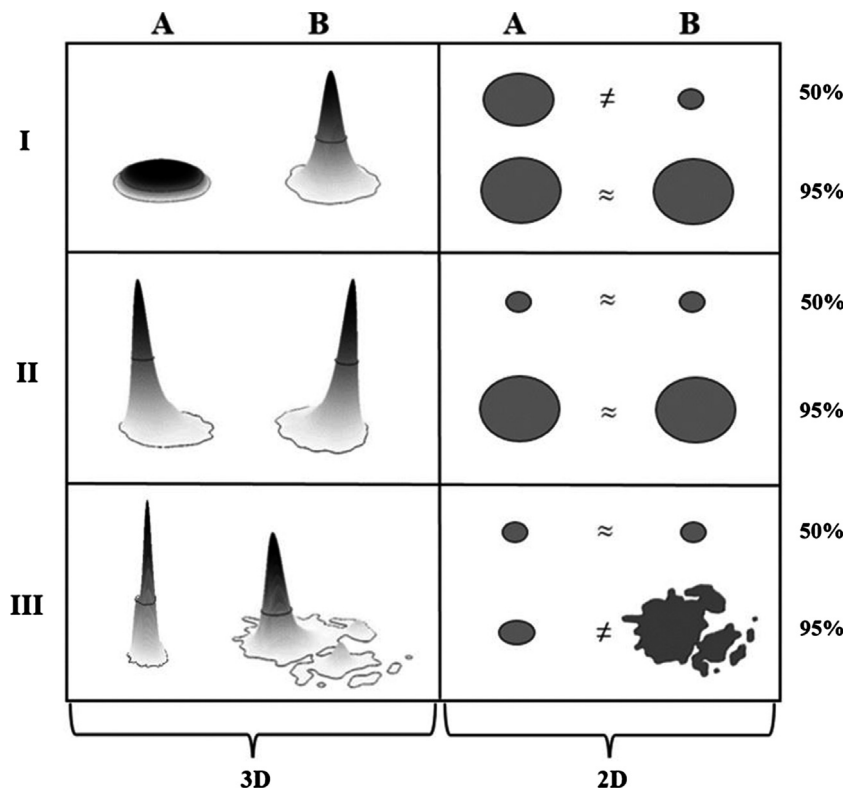
use within the extent of the home range. These estimates are commonly represented through a cell-based output known as a utilization distribution (UD; Van Winkle 1975; Worton 1989). Animals rarely utilize the area within a home range extent in a uniform pattern, but rather select areas based on various requirements, exhibiting nonrandom movements within the home range (Burt 1943). Accordingly, UD's provide information about the spatial extent of the animal's home range as well as a measure of the spatial intensity of use, where core use areas are defined as portions of the home range that exceed equal-use patterns (Samuel et al. 1985).

The estimated values of intensity of use allocated to the cells within a UD can be used to create a three-dimensional representation of the home range; a dynamic surface where the volume of the area under the plane is comprised of relative cell values that sum to 1. Compar-

isons among home ranges, particularly contrasting the extent of home ranges, are often conducted at chosen home range proportions of the volume of three-dimensional utilization distributions. These isopleths, or contours of the UD, can also be used to determine core ranges (Börger et al. 2006). Isopleths are typically defined at 50% (core home range) and 95% (total home range extent) levels (e.g., Ostfeld 1986; Heupel et al. 2004; Kie et al. 2010; Garitano-Zavala et al. 2013) for individual animals, or for all marked animals in a sample to gain population inference (Fieberg and Börger 2012). However, applying a home range estimator that quantifies intensity of use through a UD allows visual inspection across all proportional levels of the home range. It may be seen, then, that two-dimensional comparisons of estimated home range extent conducted at chosen isopleths may overlook or exclude variability in the intensity of use across the entirety of the home range that is provided by the UD (Kernohan et al. 2001; Millsbaugh et al. 2004; Kie et al. 2010). Conceptual examples of these ideas are provided in Figure 1. These exaggerated examples show obvious differences in intensity of use through various representations of home range comparisons at 50 and 95% isopleths. However, empirical high-volume GPS data used to generate UDs often result in complex distributions with disconnected polygons that can make interpretation difficult.

A suite of metrics have been developed to compare home ranges, dependent on the ecological question associated with the analysis. Fieberg and Kochanny (2005) provide detailed discussion on the use and efficacy of many of these comparative metrics. If individual animals are used as the experimental unit for comparisons, challenges arise on how to quantify and summarize population-level estimates while incorporating individual variability, regardless of the metric used for comparisons. In other words, it is relatively simple to overlay UDs to visually inspect and identify distributional changes, but it becomes increasingly difficult to compile and summarize multiple comparisons to gain population-level inference without losing detail within each experimental unit. Researchers encourage the use of the individual as the experimental unit, especially within resource selection studies (Thomas and Taylor 2006), and sampling multiple individuals is an effective method to gain population-level inference of space use (Powell and Mitchell 2012).

Our objective was to expand the application of a modern home range estimator and well-established UD comparative measures to comprehensively evaluate distributional shifts (i.e., changes in space use) across home range levels and to summarize individual comparisons to gain population-level inference on changes in home range size, overlap, and similarity. We assessed home ranges of 16 bighorn sheep (*Ovis canadensis*) to investigate changes



**Figure 1.** Conceptual examples of home range comparisons at 50 and 95% isopleth values in two- and three-dimensional aspects. (A) and (B) represent the UDs being compared in each scenario. (I) Comparison between full home range estimates (95%) indicates little difference in home range size, but on closer inspection of the UD, the intensity of use shows a marked change in core area use (50%). (II) A scenario where the full extent and core home range sizes are nearly identical, but the intensity of use has shifted. (III) Extent of 95% home range indicates a marked expansion in space use, but on closer inspection of the UD, the majority of 50% core use area remains basically unchanged.

in comparative measures when examined across UD isopleths. Researchers should find utility in expanding standard comparative home range analyses to gain a more comprehensive evaluation of distributional shifts. In particular, we demonstrate opportunities to assess linear trends that develop when comparing home range UDs across isopleths, better describing changes in animal space use.

## Materials and Methods

### Example data

As an example, we describe the process implemented to compare distributions of 16 bighorn sheep using 38,023 locations from GPS data collected before (2009–2011) and after (2011–2013) fire-mediated habitat alterations in the Seminoe Mountains in south-central Wyoming, USA. Helicopter net-gunning was used to capture all bighorn sheep, which were restrained using front and rear leg hobbles and blindfolded to minimize stress during processing. Biological samples were taken from each captured bighorn for disease and parasite screening, and each animal underwent a physical examination by trained animal handlers or a state veterinarian that included documentation of age, sex, and physical abnormalities. Animals were marked using self-piercing metal or plastic ear tags unless previous ear tags were evident. Store-on-board GPS transmitters (GENIII, model TGW3500; Telonics, Inc., Mesa, AZ or model G2110D; Advanced Telemetry Systems, Inc., Isanti, MN) attached to bighorn sheep collected location data prior to the initiation of fires that occurred in early May 2011 (prefire), and subsequent recapture of these animals continued data collection through June 2013 (postfire). This resulted in “paired” datasets, acquired from GPS location data collected from the same individuals before and after fires. All bighorn sheep captures were conducted in adherence with approved protocols (Oregon Department of Fish and Wildlife, see Foster (2005); Wyoming Game and Fish Department, Chapter 10-1535 and Chapter 33-750 permits; University of Wyoming Institutional Animal Care and Use Committee protocol 12012011).

We used the “BBMM” package (Nielson et al. 2013) in the R statistical environment (R Development Core Team 2012) to create a pair of UDs to be compared for each bighorn sheep (i.e., our experimental units). Brownian Bridge Movement Models (BBMMs) have gained in popularity due to incorporation of estimated animal motion variance, GPS error, and the time and distance between successive locations to provide a cell-based output that estimates probability of occurrence across a landscape (Bullard 1999; Horne et al. 2007). The ever-increasing

volume and detail of GPS data that challenge less-modern home range estimators (Kie et al. 2010) are often utilized within BBMMs to estimate home ranges and map migration paths using fine-scale location data. BBMMs are dependent on sequential, autocorrelated location data, and therefore are quantified on an individual basis. Although not unique to the BBMM estimator, individual home range estimates allow the use of each animal as an experimental unit, alleviating the risk of individuals with high-volume locations influencing distribution at a population level when pooling location data and using a density estimator. Overall, an array of home range estimators can provide quality UD representation. While we do not advocate for any specific estimator, we found the BBMM estimator applied well to our specific dataset.

### Estimator standardization

When conducting home range comparisons, it is important to minimize error by standardizing sampling regimes and parameters of the chosen home range estimator (Fieberg and Börger 2012). Accordingly, within a BBMM characterized by uniform distances between locations, as the temporal duration between consecutive locations increases, the probability of random movement away from the direct path between sequential locations also increases. This increase in animal motion variance results in an expansion of the resulting utilization distribution (Horne et al. 2007). Because GPS collars were programmed to collect location data either every 1 or 5 h, we standardized GPS data by selecting every fifth location from 1-h fix rates, matching the maximum fix rate schedule of transmitters from all captures. The resulting 5-h fix rate was used to ensure animal motion variance was calculated using consistent fix rates among all datasets. GPS fix rate success was high for animals in our sample (mean > 90%); even so, we set parameters of the home range estimator to censor bridges with an associated time lag exceeding 305 min to ensure models did not inflate estimated space use if intervals exceeded 5 h. We also censored initial location data from captured individuals by removing locations associated with sporadic animal movements following releases to allow for adequate temporal acclimation after releases (mean = 20.6 days, SE = 3.9 days, range = 0–70 days; see Clapp et al. 2014).

We set parameters of the home range estimator function to define a consistent spatial extent for each paired dataset that encompassed all animal locations for both prefire and postfire durations. We set a  $30 \times 30$  m cell size output to overlap paired BBMM utilization distributions and to subsequently conduct effective cell-by-cell calculations. We rounded probabilities to machine precision to define contours of each home range estimate (cell

values  $<1 e^{-15}$  rounded to zero; Fieberg and Kochanny 2005) because the Brownian bridge estimator is based on a Gaussian distribution where the probability of occurrence infinitely approaches zero. Because GPS data acquired from some individuals were less than a full calendar year in duration, we standardized each pair of model outputs using only data collected during identical timeframes, by ordinal date, for each pair of home range estimates. For example, if a prefire UD was estimated using location data collected only from 15 December through 1 June, we restricted the corresponding postfire UD to incorporate only location data collected during the same period. Although the distribution of some animals may be dependent on season, sex, and in relation to habitat components, we used the standardization of least common timeframe where adequate paired data were gathered to estimate overall annual home range differences.

### Utilization distribution comparisons

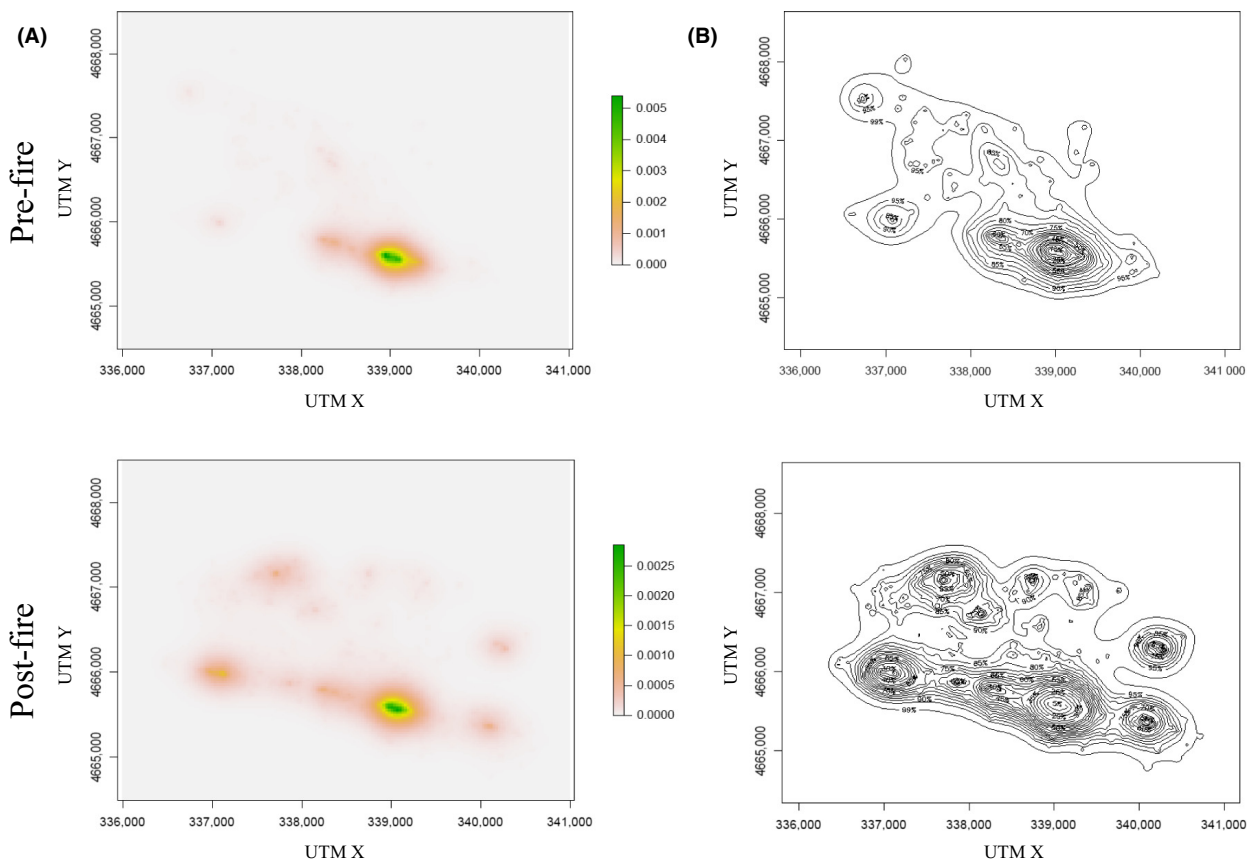
It is advantageous to apply multiple metrics and methods when analyzing and comparing home range data (Fieberg and Börger 2012). Therefore, we calculated a suite of comparative measures (Table 1) and report a chosen subset that assessed distributional changes in relation to (1) changes in home range size, (2) proportion of home range overlap, and (3) similarity between UDs. Similarity between paired utilization distributions were reported using two indices. The utilization distribution overlap index (UDOI; Fieberg and Kochanny 2005) incorporates the cumulative sum of product-based cell-by-cell calculations as well as the area of overlap between distributions, and many studies have used the UDOI index to estimate joint-space use (e.g., Berger and Gese 2007; Pauli and Peery 2012; Thiebot et al. 2012). Fieberg and Kochanny

(2005) found that while UDOI may best estimate the degree for which two animals share the same space, the product-based Bhattacharyya's affinity index (BA; Bhattacharyya 1943) may be more appropriate to compare overall similarity between utilization distributions; therefore, we reported both indices to compare distributions. Volume of intersection (VI) is another commonly used index that uses the cumulative sum of the minimum volume of intersection for corresponding cells between UDs to estimate similarity, but product-based estimators such as BA tend to outperform this index (Fieberg and Kochanny 2005). In addition, high correlation between VI and BA indices (Kochanny et al. 2008) results in similar trends when comparing UDs across home range levels; therefore, VI was not reported.

We used the `bbmm.contour` function (package `BBMM`) to identify proportional contour levels for each UD ranging from 99% (most inclusive home range estimate) to 5% (highest core use areas) in 5% intervals (Fig. 2). We stored the relative probability threshold values that represented each contour level for each UD. We then overlaid each pair of utilization distributions for visual inspection (Fig. 3). Because variation in probability of use, home range size, overlap, and similarity depend largely on the chosen contour of the UD examined, we summarized data based on multiple contour levels of the home ranges. We quantified comparative metrics starting with the most inclusive home range contour (99% isopleth) for each experimental unit. After calculating metrics at the broadest home range level, we used the appropriate probability threshold values to reclassify both prefire and postfire UD rasters at the next sequential contour level (95% isopleth). We used a conditional statement to set cell values less than the 95% contour threshold to zero. Because the remaining cell values must sum to one to remain a relative utilization distribution, we reclassified cells by divid-

**Table 1.** Common metrics used to compare home range estimates (see Fieberg and Kochanny 2005). Within the equations,  $A_x$  represents the area of the respective home range,  $A_{1,2}$  represents the area of overlap between home ranges, and  $dx dy$  indicates that cell-based computations are applied to corresponding cells for each UD.

Comparative metric	Explanation	Typical representation	Equation
Size	Proportional change in home range size	2D	$A_2/A_1$
Overlap	Proportion of HR overlap (directional)	2D	$A_{1,2}/A_x$
Volume of intersection (VI)	Minimum joint-space use between UDs	3D	$\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \min[\widehat{UD}_1(x,y), \widehat{UD}_2(x,y)] dx dy$
Bhattacharyya's affinity (BA)	Product-based UD similarity index	3D	$\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \sqrt{\widehat{UD}_1(x,y)} \times \sqrt{\widehat{UD}_2(x,y)} dx dy$
Hellinger's distance (HD)	Index of relative distance between UDs	3D	$HD = 2 \times (1 - BA)$
Utilization distribution overlap index (UDOI)	Product-based index of degree of joint-space use	3D	$A_{1,2} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \widehat{UD}_1(x,y) \times \widehat{UD}_2(x,y) dx dy$



**Figure 2.** Example showing Brownian bridge utilization distribution rasters (A) and associated contour lines (B) before (2009–2011) and after (2011–2013) fire-mediated habitat alterations for an individual female bighorn sheep. Color scales (A) represent the relative intensity of use estimated for cells within the UDs.

ing each cell value by the sum of the remaining cell values within the UD. We then recalculated comparative metrics at this level.

We repeated this process at each home range level in 5% intervals until we reached the highest defined intensity of use for the original UDs (5% isopleth). We summarized these comparisons for all individuals to quantify population-level distributional shifts across home range levels. We report trend data as mean and 95% point-wise confidence intervals using a *t*-distribution for each comparative metric or similarity index. We conducted statistical analyses and data management in R 2.15.3 (R Development Core Team 2012).

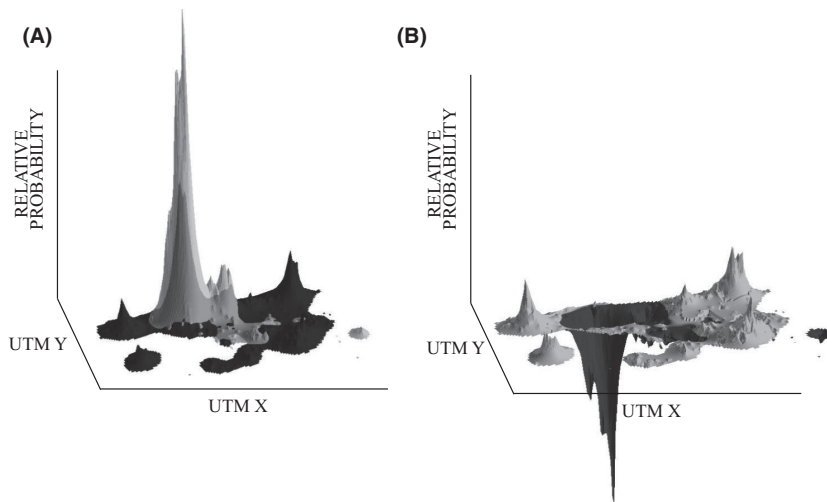
## Results

By examining individual trends across home range contours, variation was identified among individual UD comparisons (Fig. 4A), providing insight into how individuals included in the sample may influence mean distributional changes. For example, some bighorn sheep completely

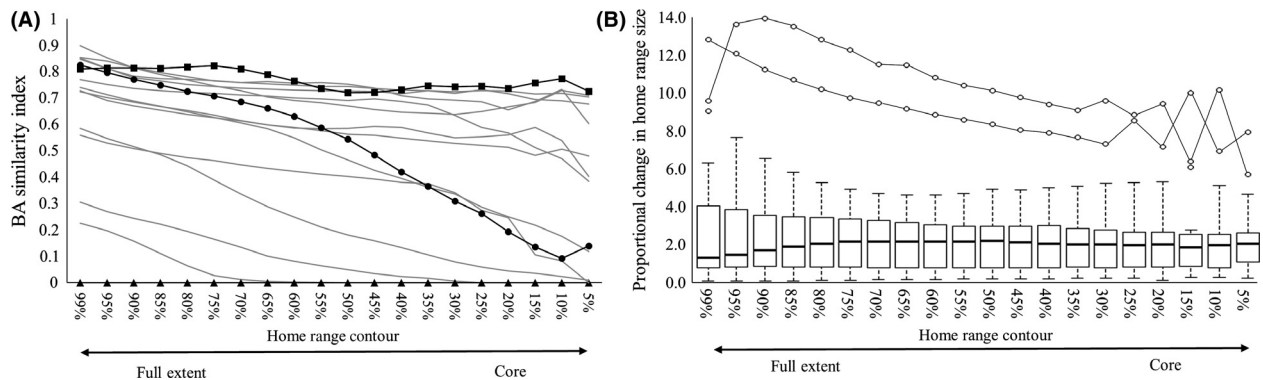
shifted home ranges after fires, exhibiting no overlap or similarity during comparisons. In addition, it was evident that a few bighorn sheep showed extreme home range changes, with comparative values >1.5 times the interquartile range of the sample, and were identified as outliers shown in box plots plotted at each contour (Fig. 4B). However, without reason to suspect outliers were influenced differently from others in the sample, we retained all animals when summarizing population-level changes.

When summarizing comparative measures to gain population-level inference, results from our example showed an approximate 200% increase in home range size consistently from the full home range extent (mean = 3.35, 95% CI = 1.16–5.53) to the highest intensity of use (mean = 2.58, 95% CI = 1.44–3.72) or core range areas (Fig. 5A). Because the change in home range size was quantified by dividing postfire by prefire area, a metric equal to 1 indicated no relative change, and confidence intervals did not overlap 1 at any home range contour. When comparing how much postfire home range area overlapped prefire area, at the 99% level home ranges





**Figure 3.** Three-dimensional representation of a female bighorn sheep UD surface overlay. (A) Overlay of surfaces prefire (2009–2011; light) and postfire (2011–2013; dark). Note that due to the relative probability of occurrence, postfire distribution expanded at the expense of a decrease in prefire core area use (moderately gray area where light and dark overlap). (B) UD surface showing difference in probability of occurrence after fires. Areas that increased in use after fires are positive and shown light, whereas areas that decreased in use are represented as dark shaded depressions (i.e., negative).

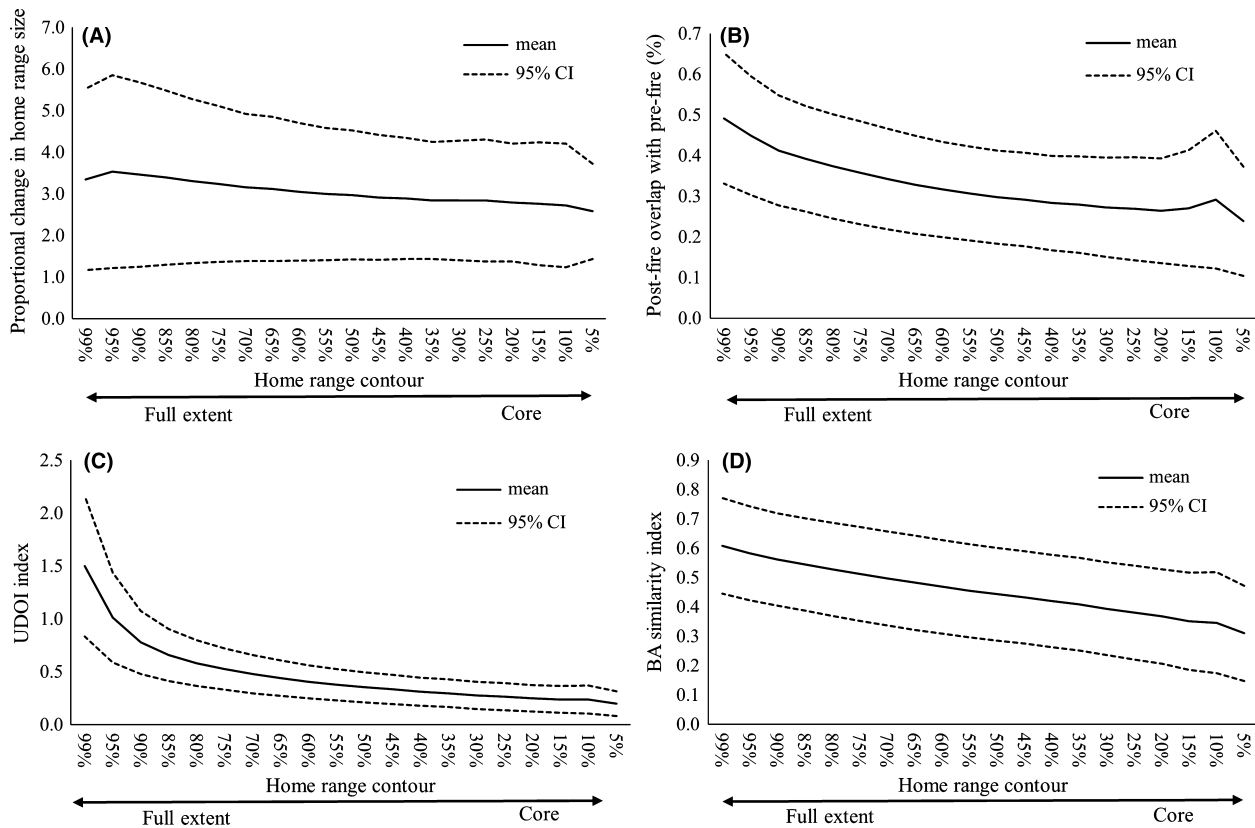


**Figure 4.** Examples of individual variation when comparing UD across home range contours for bighorn sheep ( $n = 16$ ) before (2009–2011) and after (2011–2013) fire-mediated habitat alterations. (A) Trends in BA similarity across contours for individual bighorn sheep. Note the variability among individuals includes consistently high similarity (e.g., bolded individual trend with square markers), marked decreases in similarity at increasing core home range isopleths (e.g., circle markers), and an individual with no similarity measured across contours (triangle markers). (B) Box plots constructed at each contour showing variation in the proportional change in home range size for bighorn sheep. Box plots include the interquartile range (25th–75th percentile) of comparative values; horizontal lines within boxes are median values; whiskers are 1.5 times the interquartile range. Note individual outlier comparative values were consistently  $>1.5$  times the interquartile range (connected circle markers).

averaged ~50% overlap (mean = 0.49, 95% CI = 0.33–0.65). This trend decreased to ~25% overlap (mean = 0.24, 95% CI = 0.10–0.37) at extreme core range levels (Fig. 5B). When examining similarity between UD, we identified a sharp decrease in estimated joint-space use (UDOJ) ranging from the 99% contour (mean = 1.50, 95% CI = 0.83–2.16) until an apparent “threshold” was reached at approximately the 70% isopleth (mean = 0.48, 95% CI = 0.30–0.66) after which the decline slowed as UDOI moved toward an asymptote (Fig. 5C). Using the BA index, we found mean similarity in distributions exhibited a linear decrease at increasing core range contours (Fig. 5D). Mean BA values indicated ~60% similarity at the 99% contour, trending down to only ~30% at core home range levels.

## Discussion

Results from our example allowed easy identification of bighorn sheep uniformly expanding postfire home range area across isopleth levels, with increasing space use after fire exhibited at the expense of lower intensity of use within prefire core areas. When examining home range overlap, bighorn sheep also exhibited a change in the proportion of postfire distribution that overlapped the corresponding prefire distribution in a decreasing trend from approximately 50% to 25% at increasing core range isopleths (Fig. 5B). This proportion of overlap was likely influenced by the increase in home range size, with much prefire distribution within the extent of postfire areas. Notwithstanding, we identified a relative expansion that



**Figure 5.** Distributional comparisons of 16 bighorn sheep across home range contours before (2009–2011) and after (2011–2013) fire-mediated habitat alterations. (A) Proportional change in home range size. Because the change in home range size was quantified by dividing postfire by prefire area, a metric equal to one indicates no change. (B) Proportion of postfire home ranges that overlapped pre-fire distributions. (C) Joint-space use calculated with utilization distribution overlap index (UDOI) between prefire and postfire UD. (D) Bhattacharyya’s affinity index (BA) showing overall similarity between distributions.

increased proportionally across increasing core area levels (Fig. 5B). The change in UDOI values that dropped precipitously from the 99% contour concurred with what was shown in the proportion of overlap (Fig. 5C) because UDOI was calculated using joint-space use as well as area of overlap between UD (which showed relatively high overlap at more inclusive home range levels; Fig. 5B). The BA index also showed a decrease in UD similarity at increasing core range isopleths, indicating that core home ranges were altered to a higher degree than full home range extents (Fig. 5D).

We investigated a simple approach to assess changes in utilization distributions and found notable benefits from conducting UD comparisons individually and across home range levels. By conducting paired comparisons using the individual animal as the experimental unit, outliers and individual variation were easily identified, which otherwise may have gone unnoticed if we pooled or averaged distributions across animals (Fig. 4B). Also, instances where individuals completely realigned home

ranges were apparent in overlap and similarity analyses, and by identifying these animals, we found comparisons typically shifted to lower mean proportion or similarity index values, but rendered the trend across home range levels unchanged.

The changes we identified across home range levels suggest broader questions about properly estimating the extent of home ranges. Home range extents are often chosen at a contour that encompasses a selected percentage of total space used (Anderson 1982), but appropriate levels may be difficult to quantify. Similarly, Fieberg and Börger (2012) found it unfortunate that most studies used ad hoc definitions to delineate core areas (e.g., 50% isopleth) without first considering biologically meaningful research questions and subsequently choosing commensurate analysis methods. Specifically, the size and location of core home ranges may depend on the method used to determine home range size, and substantial influences on core areas may result based on the estimated home range boundary and underlying distribution (Samuel et al.

1985). Although challenges remain to specifically identify isopleth levels that best represent core areas, conducting and summarizing comparisons across contours provided insight into how home range comparisons changed across all levels.

Ecologists are commonly faced with decisions regarding scale, and studies often report the use of multiscale approaches for replete assessments, depending on associated ecological questions (e.g., Millspaugh et al. 2004; Börger et al. 2006; Boyce 2006; DeCesare et al. 2012). By comparing home range estimates across levels, we identified thresholds in isopleth values that resulted in marked differences in home range estimates. For example, we found that mean UDOI values showed overlap in 95% confidence intervals from the 99% isopleth level (95% CI = 0.83–2.16) to the 85% level (95% CI = 0.41–0.91), while lower isopleth levels were significantly different from comparisons at the full home range extent (Fig. 5C). These results revealed how measures of similarity can change across isopleth levels – not necessarily at only 95 and 50% levels. In our example, the UDOI index indicated that isopleths greater than ~70% may not be as biologically meaningful for similarity comparisons as those <70%, where a downward trend existed, but toward an asymptote that may better represent an estimate of overall similarity. Also, core home range comparisons may potentially be influenced by restricting input that reduces the likelihood of high similarity among UD's near the peak of distributional surfaces – resulting in a typical decline in similarity index values. However, similarity can theoretically remain high at core home range levels if animals shift the extent of their distributions while sustaining uniform core area use. If desired, the ability to conduct comparative tests (e.g., *t*-test) between chosen isopleths remained. However, statistical tests are often intended to answer a specific question regarding distributional changes (e.g., “did home range area increase?”) with a definitive “yes” or “no” answer dependent on a chosen alpha value, sample size, and sample variation. We argue that given the uncertainty in extent (influenced by a chosen home range estimator) coupled with the difficulty in accurately identifying core area isopleths, assessing the trend in comparisons across isopleths better revealed not only if distributions changed, but provided insight regarding how and at what extents these changes occurred. It was also apparent that while conducting comparisons, as the home range contour decreased to include only core areas of use the potential to overlook seldom used but vital areas of the home range, such as movement corridors or migration patterns, may increase. Regardless of the chosen home range estimator or comparisons at any specific home range level, it was the ability to assess these trends in which we found the most

insight in our analysis, where we “filled the gaps” often overlooked when comparing predetermined home range contours.

When comparing across home range contours, we understand contours are not independent of each other, meaning larger home range extents influence core home range levels. This is to be expected given that comparisons are conducted among utilization distributions that are inherently reliant on correlation. Therefore, we did not consider correlation among home range levels a limitation, but that correlation across comparisons mimics correlation evident in the distributions themselves. For example, when examining a three-dimensional utilization distribution alone, we consider the ability to identify areas of increased space use a benefit, although these areas are certainly dependent upon lower levels of the distribution. In similar fashion, comparisons across isopleths inherit the correlation of the distributions, as well as the benefit to identify how distributional changes are rendered throughout. In addition, when summarizing comparisons, it is evident that all home range estimators are subject to associated error when estimating space use, some of which may be difficult to account for when averaging across animals to gain population-level inference. However, when considering the home range estimator and comparative values as consistent measurements applied to each experimental unit, identifying mean changes in measurements among UD's can describe population-level changes in space use.

Limitations exist when reclassifying UD's to conduct multilevel home range comparisons. Each reclassification decreases the number of cells within the restricted home range level, and this change could influence the results of the comparative measures. Therefore, an appropriate resolution (cell size) should be identified prior to conducting home range comparisons. For example, a tradeoff develops when calculating cell-based UD's at high resolution (e.g., 1 × 1 m) using complex home range estimators such as the BBMM. These are computationally challenging for many systems and require extensive time to calculate, even at fast processing speeds. However, at coarse resolutions (e.g., 100 × 100 m), the accuracy of comparative measures, particularly at highly concentrated contour levels (e.g., 5% core home range may encompass a small area), may not yield desired accuracy. Overall, the method we used compared UD's at differing home range levels, but did not change the resolution of the cell size as home range contour restrictions occurred. It also should be noted that other methods to calculate comparative metrics exist, especially tailored for comparing independent distributions. For example, the “adehabitat” package (Calenge 2006) in the R statistical environment (R Development Core Team 2012) is often used to conduct com-



parisons based on a kernel density UD at a desired contour. This method provides a matrix output that shows UD comparisons among multiple animal or population UDs. However, we found it advantageous to reclassify and compare space use repeatedly for the same experimental unit at multiple contours when comparing paired distributions, allowing a more comprehensive evaluation of distributional changes.

In conclusion, we compared UDs using paired data from the same animals before and after habitat alterations, but other useful applications may include comparing diurnal and nocturnal animal movement patterns, comparing seasonal migrations patterns, or identifying changes in distributions due to anthropogenic disturbances. Using paired data allowed us to summarize UD changes while estimating individual variation in comparative metrics. However, multilevel assessments across home range contours may be conducted using separate datasets to investigate space use by competing species, predator and prey systems, or invasive and native species, informing animal space use across scales for a variety of ecological questions. We found a more comprehensive evaluation of distributional changes can be identified using well-established techniques readily available to researchers – carried out by simply applying these techniques across home range scales and summarizing data to identify trends in distributional response. The benefit of the utilization distribution is that it represents spatial variation in intensity of use for the entire home range. Our analysis allowed comparative metrics to be represented and interpreted in similar fashion across all home range levels, providing an in-depth evaluation of changes in animal space use.

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## Conflict of Interest

None declared.

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