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Authors: JOHN FIEBERG, and CHRISTOPHER O. KOCHANNY

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Research and Management Viewpoint

QUANTIFYING HOME-RANGE OVERLAP: THE IMPORTANCE OF THE UTILIZATION DISTRIBUTION

JOHN FIEBERG,[1] Minnesota Department of Natural Resources, 5463-C W. Broadway, Forest Lake, MN 55025, USA
CHRISTOPHER O. KOCHANNY,[2] Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St. Paul, MN 55108, USA

Abstract: The concept of an animal's home range has evolved over time, as have methods for estimating home-range size and shape. Recently, home-range estimation methods have focused on estimating an animal's utilization distribution (UD; i.e., the probability distribution defining the animal's use of space). We illustrate the importance of the utilization distribution in characterizing the degree of overlap between home ranges (e.g., when assessing site fidelity or space-use sharing among individuals). We compare several different statistics for their ability to accurately rank paired examples in terms of their degree of overlap. These examples illustrate limitations of indices commonly used to quantify home-range overlap and suggest that new overlap indices that are a function of the UD are likely to be more informative. We suggest 2 new statistics for measuring home-range overlap: (1) for a measure of space-use sharing, we suggest a generalization of Hurlbert's (1978) $E/E_{uniform}$ statistic, which we term the utilization distribution overlap index (UDOI), and (2) for a general measure of similarity between UD estimates, we suggest Bhattacharyya's affinity (BA; Bhattacharyya 1943). Using a short simulation study, we found that overlap indices can accurately rank pairs of UDs in terms of the extent of overlap, but estimates of overlap indices are likely to be biased. The extent of the bias depended on sample size and the degree of overlap (UDs with a high degree of overlap resulted in statistics that were more biased [low]), suggesting that comparisons across studies may be problematic. We illustrate the use of overlap indices to quantify the degree of similarity among UD estimates obtained using 2 different data collection methods (Global Positioning Systems [GPS] and very high frequency [VHF] radiotelemetry) for an adult female northern white-tailed deer (*Odocoileus virginianus*) in north-central Minnesota.

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Key words: Bhattacharyya's affinity, Global Positioning System, home range, overlap, static interaction analysis, telemetry, utilization distribution, utilization distribution overlap index, volume of intersection statistic.

Recent technological advances in telemetry equipment allow wildlife researchers to collect substantially larger spatial location data sets with greater precision. In addition, new analytical techniques for analyzing telemetry data have changed the way wildlife researchers study animal movement and habitat selection. For example, the concept of an animal's home range has evolved from Burt's (1943:351) largely verbal definition, "that area traversed by the individual in its normal activities of food gathering, mating and caring for young," to a more quantitative definition in terms of the animal's utilization distribution (UD), i.e., the probability distribution defining the animal's use of space (Van Winkle 1975). A commonly recognized definition of an animal's home range is the smallest area associated with a 95% probability of finding the animal (White and Garrott 1990). The UD provides a useful summary of space use for a given individual, and therefore, we might expect the UD to play a key role in other types of analyses using telemetry data. For example, the UD may provide the most informative measure of use in habitat selection studies (Marzluff et al. 2001, 2004). In addition, consideration of the UD when measuring the degree of space-use sharing among individuals or the degree of site fidelity for an individual across years or seasons can lead to more informative measures of home-range overlap (Seidel 1992, Millspaugh et al. 2004).

Interest in quantifying home-range overlap or space-use sharing between animals or for the same animal at different temporal points (e.g., seasons) has increased in recent years (Seidel 1992; Millspaugh et al. 2000, 2004; Kernohan et al. 2001). When simultaneous observations of animal locations are available, it is possible to assess the degree of dynamic interaction between individuals by comparing the temporal sequence of their movement paths (Macdonald et al. 1980, Kernohan et al. 2001). We consider the more common situation in which simultaneous observations are not available, and therefore a static interaction analysis is performed in which the sets of locations are compared without reference to the

[1] E-mail: John.Fieberg@dnr.state.mn.us
[2] Present address: Advanced Telemetry Systems, Inc., 470 First Avenue North, Isanti, MN 55040, USA.

temporal sequence of locations (Macdonald et al. 1980, Kernohan et al. 2001). One can test for significant differences in the distribution of groups of locations in space using permutation procedures (Mielke and Berry 1982, Bioondini 1988). However, a measure of the degree of overlap is often desirable. While a few different indices have been proposed for quantifying home-range overlap, these indices have rarely been compared (Millspaugh et al. 2004).

Our goal is to provide a comparative review of commonly used overlap indices. First, we review metrics used to quantify home-range overlap and suggest alternative indices for accomplishing this objective. We then use a series of paired examples to illustrate computation of these indices and to facilitate their comparison. These examples illustrate some limitations of indices commonly used to quantify home-range overlap and suggest that new overlap indices that utilize UD estimates are likely to be more informative. We then assess the properties of the indices using a simulation study. Lastly, we illustrate the use of these indices to quantify the degree of similarity among UD estimates obtained using 2 different data collection methods (GPS vs. triangulation with VHF radiocollars) for an adult female northern white-tailed deer (*Odocoileus virginianus*) in north-central Minnesota. In the sections that follow we refer to animal i and animal j when discussing overlap indices. However, the same methods may be used to quantify site fidelity by replacing animal i and animal j with time period i and time period j.

INDICES OF OVERLAP

The simplest methods for quantifying static overlap only consider the spatial domain of the individual home ranges and ignore the relative probability of use (i.e., the UD). For example, home-range estimates may be overlaid, and the percent overlap may be used to quantify the degree of fidelity (White and Garrott 1990, Mizutani and Jewel 1998, Kernohan et al. 2001). Following the notation of Kernohan et al. (2001):

$$HR_{i,j} = A_{i,j} / A_i \tag{1}$$

where $HR_{i,j}$ is the proportion of animal i's home range that is overlapped by animal j's home range, A_i is the area of animal i's home range, and $A_{i,j}$ is the area of overlap between the 2 animals' home ranges. Typically, $HR_{i,j} \neq HR_{j,i}$ (i.e., the indices are directional); therefore, the degree of overlap is best quantified using $HR_{i,j}$ and $HR_{j,i}$. These measures are easy to interpret, and they can be applied to home-range estimates that do not rely on an estimate of the UD (e.g., home-range estimates calculated using the minimum convex polygon; Kernohan et al. 2001). However, as Kernohan et al. (2001) illustrate, these measures can lead to misleading conclusions, particularly when applied to estimates of home range obtained using the minimum convex polygon method. In particular, because these methods do not take into account the individuals' utilization distributions, they may result in large estimates of overlap even though the probability of finding the 2 animals in the same general area is quite small.

Ostfeld (1986) suggested extending eq (1) using a weighted combination of area overlap between core areas (defined by 50% probability contours) and high-use areas (defined by 95% contours). However, a more straightforward alternative when estimates of UDs are available is to construct probabilistic measures similar to eq (1). Let $\hat{UD}_i$ be the estimated UD for animal i and $\hat{UD}_j$ the estimated UD for animal j. Further, assume that UD_i is >0 only in A_i and UD_j is >0 only in A_j. In other words, A_i and A_j represent the full extent of spatial use for animals i and j. The metrics defined by eq (1) are easily extended to allow for nonrandom use of animal j's home range by animal i and vice versa. Rather than measure the proportion of animal i's home range overlapped by animal j, one can calculate the probability of animal j being located in animal i's home range, $PHR_{i,j}$:

$$PHR_{i,j} = \iint_{A_i} \hat{UD}_j(x, y)\, dxdy \tag{2}$$

$PHR_{i,j}$ and $PHR_{j,i}$ will be equivalent to $HR_{i,j}$ and $HR_{j,i}$ when the habitat utilization distributions are constant across space for both individuals (i.e., when UD_i is a uniform distribution for i = 1, 2). Similar measures using grid cell counts have been proposed by Smith and Dobson (1994).

These measures can be modified for home ranges based on smaller probability contours (e.g., a 95% probability contour or a 50% probability contour). Let $A_{i,p}$ denote the area associated with animal i's home range as defined by the pth probability contour of UD_i, and let $\hat{UD}_{i,p}$ denote the estimated conditional UD for animal i (i.e., the probability distribution for animal i given that it is in $A_{i,p}$):

$$\hat{UD}_{i,p}(x, y) = \begin{cases} 0 \text{ if } (x, y) \notin A_{i,p} \\ \hat{UD}_i(x, y) \;/\; p \text{ if } (x, y) \in A_{i,p} \end{cases} \tag{3}$$

By replacing the UD's in eq (2) with the conditional UDs from eq (3), we can calculate appropriate overlap indices that limit inference to home ranges defined by smaller probability contours. For example, the probability of animal *i* being in animal *j*'s 50% core area given that animal *i* is in its own 50% core area can be estimated using:

$$PHR_{j,i} = \iint_{A_{j,50}} \hat{\mathrm{UD}}_{i,50}(x, y)\,dxdy \quad (4)$$

Similarly, the probability that animal *i* is in animal *j*'s 95% home range, given that animal *i* is in its own core area can be estimated by integrating the above expression over $A_{j,95}$ rather than $A_{j,50}$.

One disadvantage of equations 1–3 is that 2 separate measures are required to quantify overlap rather than a single (nondirectional) measure that reflects the degree of similarity in the 2 animals' UDs. Alternatively, Rasmussen (1980) suggested applying Spearman's correlation coefficient (Zar 1996), r_s, to nonparametric estimates of the UDs obtained using a grid cell method (White and Garrott 1990). Kernohan et al. (2001) discussed some of the limitations of this approach. In particular, the results would be dependent upon the grid cell size used to estimate the UD. Difficulty in choosing an appropriate grid cell size is likely responsible for the relative unpopularity of grid cell methods for home-range analysis. There are other disadvantages of using Rasmussen's (1980) approach that we illustrate in the next section.

An alternative statistic that utilizes the UD estimates for both animals, the volume of intersection statistic or VI index (VI), was first suggested by Seidel (1992) and later recommended by Kernohan et al. (2001):

$$\mathrm{VI} = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} min[\hat{\mathrm{UD}}_1(x,y), \hat{\mathrm{UD}}_2(x,y)]\,dxdy \quad (5)$$

(note the min is missing in Kernohan et al. 2001 and also from Millspaugh et al. 2004). The VI index ranges between zero (for 2 home ranges with no overlap) and 1 (for 2 home ranges with the same UD). This method improved upon other measures of overlap by providing a single measure of overlap that is a function of the full UDs for both animals. The VI index has recently been applied in a variety of settings: to compare space use sharing between hunters and elk (*Cervus elaphus*; Millspaugh et al. 2000), to determine the degree to which military activities influence site fidelity for prairie falcons (*Falco mexicanus*; Marzluff et al. 2001), to measure agreement between model predictions of space use and observed telemetry data for a Rocky Mountain elk population (Roloff et al. 2001), and to compare the accuracy of different kernel-based home-range estimators (Gitzen and Millspaugh 2003).

Several other measures of similarity, dissimilarity, and overlap were proposed in ecological (Hurlbert 1978, Rao 1982) and statistical (Krzanowski 2003) literature. We consider 2 additional measures for quantifying home-range overlap: (1) Bhattacharyya's affinity (BA; Bhattacharyya 1943), a statistical measure of affinity between 2 populations, and (2) an index similar to Hurlbert's (1978) $E/E_{uniform}$ index of niche overlap, which we call the UD overlap index (UDOI). Both of these measures are functions of the product of the 2 UDs, $\mathrm{UD}_i(x, y) \times \mathrm{UD}_j(x, y)$ = the joint distribution of the 2 animals' UDs under the assumption that they use space independently of one another:

$$\mathrm{BA} = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \sqrt{\hat{\mathrm{UD}}_1(x,y)} \times \sqrt{\hat{\mathrm{UD}}_2(x,y)}\,dxdy \quad (6)$$

$$\mathrm{UDOI} = A_{1,2} \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \hat{\mathrm{UD}}_1(x,y) \times \hat{\mathrm{UD}}_2(x,y)\,dxdy \quad (7)$$

The BA statistic is related to another popular statistical measure of distance between 2 populations, Hellinger's distance (*HD*), by the following equality (Matusita 1973):

$$HD = \left[\int_{-\infty}^{\infty}\int_{-\infty}^{\infty}\left[\sqrt{\hat{\mathrm{UD}}_1(x,y)} - \sqrt{\hat{\mathrm{UD}}_2(x,y)}\right]^2 dxdy\right]^{1/2} = 2 \times (1 - \mathrm{BA}) \quad (8)$$

Like VI, BA ranges from zero (no overlap) to 1 (identical UDs). The UDOI also equals zero for 2 home ranges that do not overlap and equals 1 if both UDs are uniformly distributed and have 100% overlap. However, UDOI can be >1 if the 2 UDs are nonuniformly distributed and have a high degree of overlap. The UDOI is a modification of Hurlbert's (1978) $E/E_{uniform}$ statistic to allow for continuous spatial UDs. The biological interpretation of UDOI is similar to Hurlbert's $E/E_{uniform}$ statistic; both measure the amount of overlap relative to 2 individuals using the same space uniformly. Values <1 indicate less overlap relative to uniform space use, whereas values >1 are indicative of higher than normal overlap relative to uniform space use.

Conditional estimates of the VI, BA, and UDOI indices (similar to the conditional $PHR_{i,j}$ measures) can also be informative. For example, we can measure the degree of overlap (or similarity) for 95% home ranges or 50% core areas if we replace the $\hat{\mathrm{UD}}_i$s in equations 5–7 with the conditional UD estimates defined in eq (3).

Table 1. Home-range overlap measures for paired examples[a].

Example		$HR_{1,2}$	$HR_{2,1}$	$PHR_{1,2}$	$PHR_{2,1}$	r_s	VI	BA	UDOI
I	A*	0.75	0.75	0.75	0.75	–0.25	0.75	0.75	0.56
	B	0.75	0.75	0.20	0.75	–0.73	0.20	0.38	0.15
II	A*	0.75	0.75	0.80	0.80	0.05	0.80	0.80	1.14
	B	0.75	0.75	0.80	0.80	–0.61	0.30	0.59	0.39
III	A*	0.75	0.75	0.60	0.60	–1.00	0.40	0.55	0.30
	B	0.25	0.50	0.70	0.10	–0.78	0.10	0.26	0.07
IV	A*	0.67	0.67	0.80	0.60	–0.33	0.60	0.69	0.48
	B	0.67	0.67	0.60	0.60	–1.00	0.60	0.60	0.36
V[b]	A	1.00	1.00	1.00	1.00	NA	1.00	1.00	1.00
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.36

[a] Consecutive rows (•A & •B) make up each example, with the pair of home ranges having the (intuitively) higher degree of overlap indicated by an *.
[b] The 2 pairs should be ranked equally if a measure of UD similarity is desired, while VB should be ranked higher if a measure of space-use sharing is desired.

ÛDI COMPARISON OF OVERLAP INDICES

We compared $HR_{i,j}$, $PHR_{i,j}$, r_s, VI, BA, and UDOI using a series of 5 simple paired examples (I–V, Table 1). We chose each example to illustrate a limitation of 1 of the traditional methods. We present the examples (below) as sets of 2 × n tables, with the columns indicating spatial locations, the rows indicating separate home-range estimates, and the cell contents providing the UD for each home-range estimate at the given spatial location. Thus, we illustrate the methods using discrete UDs (i.e., the UD is assumed to be constant in each cell of the table), but the examples are also illustrative of how these statistics are likely to be calculated in practice using numerical integration (Appendix I).

Example I: The Importance of the UD

IA

UD_{1A}	0.25	0.25	0.25	0.25	0
UD_{2A}	0	0.25	0.25	0.25	0.25

IB

UD_{1B}	0.25	0.25	0.25	0.25	0
UD_{2B}	0	0.1	0.05	0.05	0.8

This first set of paired examples illustrates the importance of the UDs in characterizing overlap, using the area-based measures given in eq (1) to quantify overlap results in identical measures for the 2 examples. In IA and IB, $A_1 = A_2 = 4$ and $A_{1,2} = 3$ (assuming each grid cell has area = 1^2). Thus, $HR_{1,2} = HR_{2,1} = 0.75$. Yet, if the UDs represent different animals moving independently of one another throughout the landscape, we would be more likely to find 1A and 2A near each other than 1B and 2B. In addition, the UDs in A are much more alike than the UDs in B. Thus, overlap in A should be higher than in B, whether we desire a measure of space-use sharing or a measure of similarity among the UDs. The probabilistic measures given by eq (2) are able to capture the difference between these 2 examples. For example IA, the UDs of both animals are uniform distributions, and hence $PHR_{i,j} = HR_{i,j}$:

$$PHR_{1,2} = PHR_{2,1} = 0.25 + 0.25 + 0.25 = 0.75$$

In example IB (as in IA), $PHR_{2,1} = 0.75$. However, $PHR_{1,2} = 0.2$ $(0.1 + 0.05 + 0.05)$, indicating a relatively small probability of finding animal 2 in animal 1's home range. Thus, using the pair of indices $PHR_{1,2}$ and $PHR_{2,1}$, we would correctly conclude that the amount of overlap is greater in Example A than B. For this example, the VI, BA, and UDOI statistics also clearly indicate that the degree of overlap is greater in A than in B (Table 1). We illustrate the calculation of these indices below:

Example A: VI = min(0.25, 0.25) + min(0.25, 0.25) + min(0.25, 0.25) = 0.75

Example B: VI = min(0.25, 0.1) + min(0.25, 0.05) + min(0.25, 0.05) = 0.2

Example A: BA = $\sqrt{0.25 \times 0.25} + \sqrt{0.25 \times 0.25} + \sqrt{0.25 \times 0.25} = 0.75$

Example B: BA = $\sqrt{0.25 \times 0.1} + \sqrt{0.25 \times 0.05} + \sqrt{0.25 \times 0.05} = 0.38$

Example A: UDOI = 3 × (0.25 × 0.25 + 0.25 × 0.25 + 0.25 × 0.25) = 0.56

Example B: UDOI = 3 × (0.25 × 0.1 + 0.25 × 0.05 + 0.25 × 0.05) = 0.15

Finally, r_s is negative in both cases and larger in absolute value for example B (–0.73 vs. –0.25; Table 1). We will explore this measure further in Example III.

Example II: The Importance of Considering $\hat{UD}_1$ and $\hat{UD}_2$ Jointly

IIA

UD_{1A}	0.2	0.1	0.6	0.1	0
UD_{2A}	0	0.1	0.6	0.1	0.2

IIB

UD_{1B}	0.2	0.1	0.6	0.1	0
UD_{2B}	0	0.6	0.1	0.1	0.2

Our second example illustrates the need to consider $\hat{UD}_1$ and $\hat{UD}_2$ jointly. For this example, we focus on the probabilistic measures $PHR_{1,2}$ and $PHR_{2,1}$, VI, BA, and UDOI. If the 2 UDs represent 2 animals moving independently of each other, there would be a higher probability of finding 1A and 2A together because of the high probability of being in the third grid cell for both animals. Furthermore, the 2 UDs in A are more similar to each other than the UDs in B. Therefore, we would again hope that any measure of overlap would be higher in A than in B. However, the probabilistic measures $PHR_{i,j}$ fail to distinguish between A and B, since the total probability of finding animal 1 in animal 2's home range (and vice versa) is the same in both examples (Table 1). The $PHR_{1,2}$ only considers $\hat{UD}_2$, whereas $PHR_{2,1}$ only considers $\hat{UD}_1$ (see eq 2), and in both cases, $PHR_{1,2} = PHR_{2,1} = 0.1 + 0.6 + 0.1 = 0.8$. By contrast, the VI, BA, and UDOI statistics were able to correctly rank these 2 examples since they consider $\hat{UD}_1$ and $\hat{UD}_2$ jointly throughout the area of overlap (Table 1).

Example III: Spearman's Correlation as an Index of Overlap

IIIA

UD_{1A}	0.4	0.3	0.2	0.1	0
UD_{2A}	0.1	0.2	0.3	0.4	0

IIIB

UD_{1B}	0.4	0.3	0.2	0.1	0
UD_{2B}	0	0	0	0.7	0.3

Our third example illustrates the difficulty in interpreting r_s as a measure of overlap. We do not consider the other measures of overlap here (see Table 1). The UDs in A appear to have moderate overlap, but they are negatively correlated with $r_s = -1$. In B, there is less overlap, and the negative correlation between the 2 UDs is not quite as great ($r_s = -0.78$). Compare these examples with those from Example I. In Example I, the absolute value of r_s was higher for B than A, but the degree of overlap was higher for A than B (i.e., the relationship between r_s or $|r_s|$ and the degree of overlap is not consistent). Spearman's correlation statistic measures the linear association between the rank order probabilities of the 2 UDs across the landscape. While positive values for r_s are likely to be indicators of a high degree of overlap, these examples illustrate the difficulty in interpreting or comparing 2 negative values of r_s.

Example IV: VI versus BA and UDOI

IVA

UD_{1A}	0.3	0.3	0.4	0
UD_{2A}	0.4	0.4	0	0.2

IVB

UD_{1B}	0.3	0.3	0.4	0
UD_{2B}	0.3	0.3	0	0.4

We chose our fourth example to illustrate the better discriminatory power of the BA and UDOI statistics compared to VI. Here again, if the 2 UDs represent 2 animals moving independently of each other, there would be a higher probability of finding 1A and 2A together than 1B and 2B. In example A, animal 2 has a higher probability of being in 1 of the first 2 cells that are also a part of animal 1's home range. This effect is captured by $PHR_{1,2}$; $PHR_{1,2} = 0.8$ in A and = 0.6 in B ($PHR_{2,1}$ = 0.6 in both examples). However, VI = 0.6 for both examples. By contrast, the BA and UDOI statistics are slightly higher for A than B (Table 1). These latter indices make better use of the information in each cell by taking the product of $\hat{UD}_1$ and $\hat{UD}_2$ rather than the $\min(\hat{UD}_1, \hat{UD}_2)$; therefore, they result in more appropriate measures of overlap.

Example V: UDOI versus BA (and VI)

VA

UD_{1A}	0.2	0.2	0.2	0.2	0.2
UD_{2A}	0.2	0.2	0.2	0.2	0.2

VB

UD_{1B}	0.8	0.2	0	0	0
UD_{2B}	0.8	0.2	0	0	0

In our fifth example, we intend to illustrate the potentially better discriminatory power of the UDOI statistic relative to the BA statistic when a measure of space-use sharing is desired. In A and B the 2 UDs are identical, and in both cases, the BA and VI indices are equal to 1. However, if the 2 UDs represent 2 animals moving independently of each other, there would be a higher probability of finding 1B and 2B together (assuming that, as in the other examples, the grid cell sizes are the same in A and B). The UDOI statistic is able to capture this effect, with UDOI = 1 in A (indicating complete overlap and uniform space-use for both individuals) and 1.36 in Example B. The UDOI takes into account the degree to which the UDs are concentrated in space – resulting in a higher index in B, since both animals spend most of their time in a relatively small area relative to A, where the animals use a larger area more uniformly.

This example suggests that the UDOI may be the most appropriate index for measuring the degree to which 2 animals share the same space. On the other hand, the BA statistic might be more appropriate if the goal is to quantify the overall similarity of the 2 UDs (e.g., if the 2 animals represent 2 different estimates of the same UD). Two such applications are (1) comparing multiple, home-range estimators using the same set of data (e.g., comparing kernel-based density estimators with different smoothing parameters censu Gitzen and Millspaugh 2003), and (2) comparing 2 sets of data collected on the same individual during the same time period using different sampling methods (e.g., data collected using GPS collars vs. conventional VHF radiocollars, illustrated in a later section). In these latter applications, it is desirable that any measure of similarity be at its maximal value for both A and B, since in both examples the 2 UDs are identical. In other words, one might prefer the BA statistic to the UDOI when a measure of similarity of the 2 UDs is desired rather than a measure of space-use sharing.

SIMULATION STUDY

We conducted a short simulation study involving 4 different UDs, each constructed from a different mixture of 3 multivariate normal distributions (Table 2, Fig. 1). This simulation study mimics a scenario in which there are 3 main centers of activity used to varying degrees by 4 different animals. We consider 2 different types of overlap: (1) overlap between 2 samples of locations from the same animal, and (2) overlap between animal 1 and animals 2–4. We considered 3 sample sizes (n = 40, 150, 500), and we simulated 1,000 × 2 datasets for each UD × sample size combination. For each pair of samples, we calculated *HR*, *PHR*, VI, BA, and UDOI; we averaged $HR_{i,j}$ and $HR_{j,i}$ and $PHR_{i,j}$ and $PHR_{j,i}$ for each simulation to obtain a nondirectional overlap statistic from these pairs of indices.

We used a library of functions written by Wand and Jones (1995) in the R programming language (R Development Core Team 2003) to produce the kernel density estimates of the UDs. We used a Guassian kernel and determined optimal bandwidths (separately) in the x and y directions using the plug-in estimator (Sheather and Jones 1991). We wrote our own code to estimate home-range size and to calculate the overlap statistics (available from the first author upon request). We estimated the UDs across a 150 × 150 grid and calculated overlap indices using conditional 95% UDs (eq 3) to eliminate the effect of very small, nonzero estimates of the UDs near the boundary of the observations (Appendix I).

Table 2. Utilization distributions (UDs) considered in the simulation experiment to study the bias and precision of overlap indices. Each UD is constructed using a different mixture of 3 multivariate normal distributions (MV_1, MV_2, MV_3).

UD	MV[i]
$UD_1 = 0.8 \bullet MV_1 + 0.1 \bullet MV_2 + 0.1 \bullet MV_3$	MV_1: $\mu_1 = (10, 20)$, $\Sigma = \begin{pmatrix} 9 & 0 \\ 0 & 9 \end{pmatrix}$
$UD_2 = 0.6 \bullet MV_1 + 0.2 \bullet MV_2 + 0.2 \bullet MV_3$	MV_2: $\mu_2 = (20, 10)$, $\Sigma = \begin{pmatrix} 25 & 0 \\ 0 & 9 \end{pmatrix}$
$UD_3 = 0.4 \bullet MV_1 + 0.3 \bullet MV_2 + 0.3 \bullet MV_3$	MV_3: $\mu_3 = (20, 20)$, $\Sigma = \begin{pmatrix} 9 & -9 \\ -9 & 25 \end{pmatrix}$
$UD_4 = 0.1 \bullet MV_1 + 0.1 \bullet MV_2 + 0.8 \bullet MV_3$	

[i] All multivariate normal distributions can be uniquely defined by their mean and variance/covariance matrices (μ and Σ, respectively).

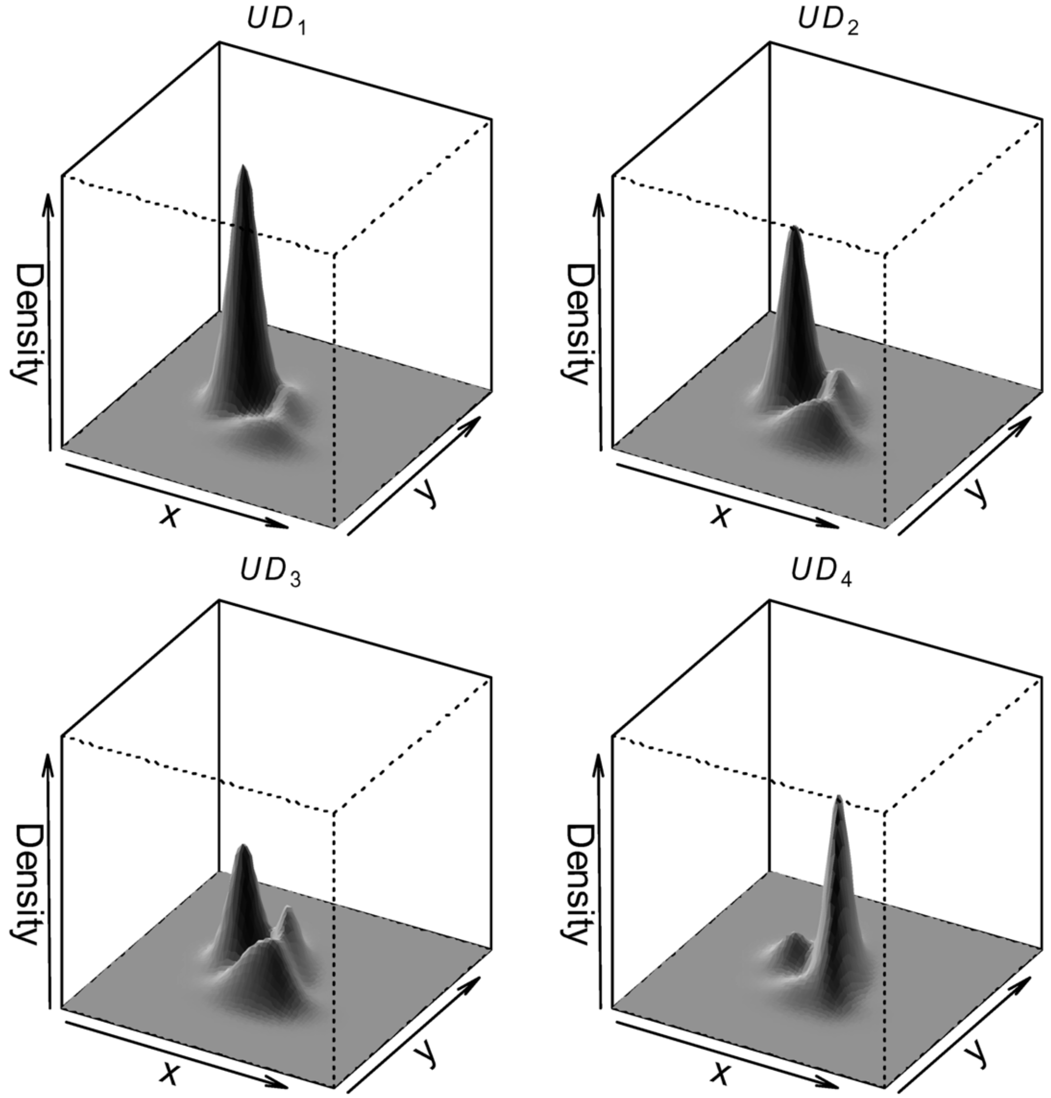

Fig. 1. Four utilization distributions (UDs) considered in the simulation experiment to study the bias and precision of overlap indices. The x and y axes represent the spatial domain utilized by the animal, while the z-axis represents the relative proportion of time spent in each spatial location (i.e., z = UD[x, y]).

The simulations illustrated some of the complexities that are expected when analyzing real data. First, estimates of overlap indices were biased low when the UDs had a high degree of overlap. If 2 samples are taken from the same UD, then all of the overlap statistics except UDOI should theoretically equal 1. However, estimates of the overlap statistics for 2 samples from the same UD never reached this bound, and estimates of the UDOI were also substantially lower than the true values determined by the true UDs (Fig. 2a–e). Estimates of overlap between UD_1 and UD_2–UD_4 were also biased low (Fig. 2f–j). On the other hand, estimates of overlap may be biased high for UDs with very little overlap (e.g., if the true overlap is 0, it is possible in small samples to observe a few locations near each other and thus obtain an estimate of overlap >0). We observed this phenomenon when attempting to estimate overlap among core areas (defined by the 50% probability contour) for UD_1 and UD_4, where the true overlap = 0 (Fieberg, Minnesota Department of

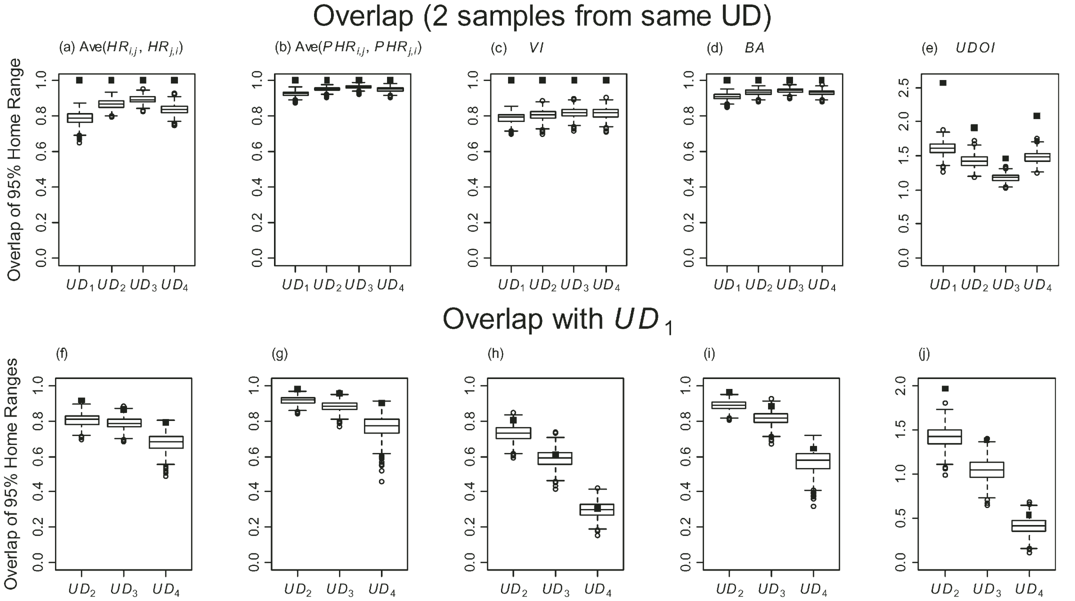

Fig. 2. Distribution of overlap statistics calculated from 1,000 samples of size n = 150; (a–e) overlap statistics calculated from 2 samples from the same utilization distribution (UD); (f–j) overlap between UD_1 and (UD_2, UD_3, UD_4). Boxes bound the 25th and 75th percentiles of the overlap statistics (across the 1,000 simulation runs), solid line within the box indicates the median, and the whiskers extend to 1.5 times the interquartile range of the observations. True values of the overlap statistics are given by solid squares.

Natural Resources,unpublished data). Similarly, Seidel (1992) observed positive biases for the VI statistic in a simulation study using UDs with a small degree of overlap (true VI < 0.4), with negative biases for larger values of VI (true VI > 0.6).

More importantly, the degree of bias appeared to depend on the underlying UDs and their true overlap indices. The sampling distributions of the overlap statistics were symmetric, and therefore the median of these distributions (indicated by the solid line in the middle of the boxplots) should be close to the mean. Thus, the extent of bias can be inferred by comparing the median of the sampling distributions to the true overlap values (indicated by the solid squares in Fig. 2 and the dotted lines in Fig. 3). For estimates of overlap between UD_1 and (UD_2, UD_3, and UD_4), the rank order of the relative bias (i.e., bias relative to the spread of the sampling distribution) followed the same pattern for each of the overlap statistics: relative bias in overlap(UD_1, UD_2) > relative bias in overlap(UD_1, UD_3) > relative bias in overlap(UD_1, UD_4; Fig. 2f–j). This ordering is also indicative of the true overlap among these distributions (listed in decreasing order). The extent of the bias depended strongly on sample size and decreased with increasing n (Fig. 3). These results suggest that comparisons of overlap indices across studies may be misleading, particularly if the studies' sample sizes vary considerably. Note again that the extent of the bias in estimates of overlap between UD_1 and UD_4 (Fig. 3f–j) was strongly dependent on the true overlap statistics, with VI having the least amount of bias and average($PHR_{1,4}$, $PHR_{4,1}$) having the most bias; the bias of other indices fell in-between these 2 extremes. This ordering correlates well with the true indices of overlap between UD_1 and UD_4 (given by the dotted lines in Fig. 3f–j; the true VI is 0.3, while the true value of average[$PHR_{1,4}$, $PHR_{4,1}$] = 0.9). Thus, while the VI appeared to give unbiased estimates of overlap between UD_1 and UD_4 (Fig. 3h), this was generally not the case (e.g., there was a substantial bias in the estimated VI for the overlap between 2 samples from the same UD [Fig. 3c] and the overlap between UD_1 and either UD_2 or UD_3 [Fig. 2h]).

For many applications, relative comparisons (e.g., estimates of overlap[UD_1, UD_2] – overlap[UD_1,UD_3]) may be of interest. We expect that estimates of these differences will again be biased since the individual components are likely to be biased to different degrees (again, depending on the true overlap measures and sample size). Furthermore, estimates of differences may be attenuated (biased towards zero) since estimates of larger (true) values of overlap tended to be more biased

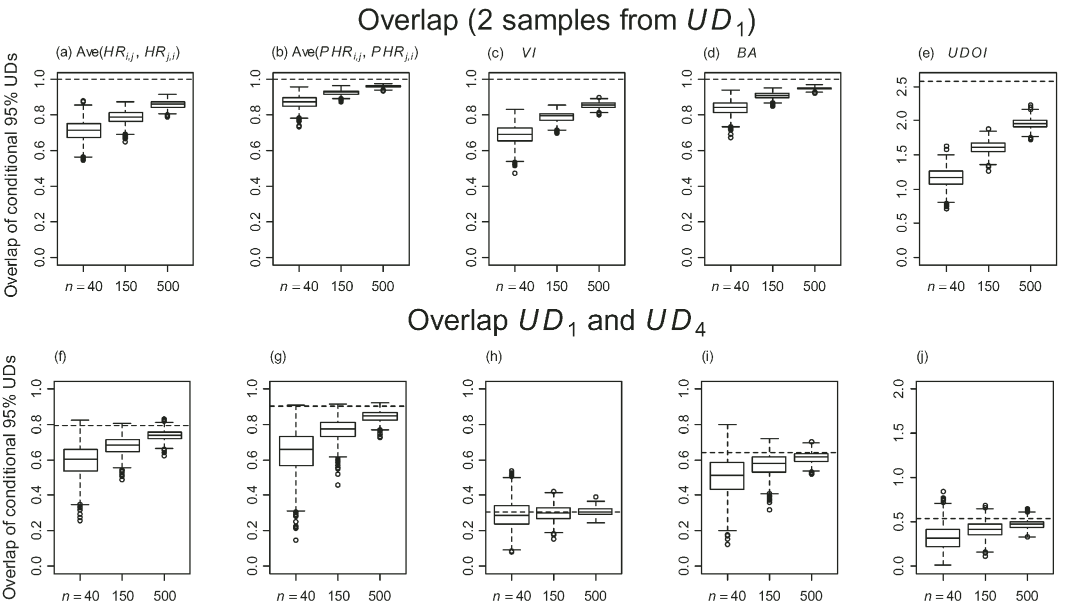

Fig. 3. Effect of sample size on the overlap statistics. Panels (a–e) illustrate the effect of increasing sample size (n = 40, 150, 500) on the sampling distribution of overlap statistics calculated from 2 samples from UD_1. Panels (f–j) illustrate the effect of increasing sample size (n = 40, 150, 500) on the sampling distribution of overlap statistics calculated from samples from UD_1 and UD_4. Dotted lines indicate the true overlap indices calculated using the true utilization distributions. Boxes bound the 25th and 75th percentiles of the overlap statistics (across 1,000 simulation runs), solid line within the box indicates the median, and the whiskers extend to 1.5 times the interquartile range of the observations.

than estimates of smaller (true) values of overlap. On the other hand, the UD-based overlap indices were usually successful in correctly ranking pairs of animals in terms of their degree of overlap (Table 3). The probability-based measures ($PHR_{i,j}$, $PHR_{j,i}$), VI, BA, and UDOI correctly ranked (overlap[UD_1, UD_2] > overlap[UD_1, UD_3] > overlap[UD_1, UD_4]) > 80% of the time when $n = 40$ and nearly 100% of the time when $n = 150$. By contrast, the area-based measures ($HR_{i,j}$, $HR_{j,i}$) gave the correct ranking in only 58% of the simulations when $n = 40$, 75% of the time with $n = 150$, and 96% of the time when $n = 500$ (Table 3). The UDOI and VI had slightly better success rates than BA and ($PHR_{i,j}$, $PHR_{j,i}$) when $n = 40$, but these indices also show greater separation in their true values for the UDs that we considered (Fig. 2f–j). Therefore, we expected these statistics to give more accurate rankings in the simulation example we considered. Overall, these results suggest that it may be possible to rank pairs of UDs in terms of overlap even if the individual measures are biased.

APPLICATION: COMPARING ESTIMATES OF HOME RANGE VIA GPS AND CONVENTIONAL VHF RADIOTELEMETRY

We captured and collared adult female white-tailed deer at Camp Ripley Army National Guard Training Site (94°15′–94°30′N and 46°05′–46°20′W) in north-central Minnesota during late January–early February of 1999 and 2000. We programmed store-on-board GPS-receiver collars (Advanced Telemetry Systems, Isanti, Minnesota, USA) to take 1 location per hour along with 2 15-minute reattempts if the initial attempt was unsuccessful. Each unit also contained a very high frequency (VHF) radio beacon that allowed deer to be monitored with conventional ground-based triangulation methods (White and Garrott 1990). Essentially, we collected 2 data sets for each animal.

Table 3. Success rate (%) of overlap indices accurately ranking overlap (UD_1, UD_2) > overlap (UD_1, UD_3) > overlap (UD_1, UD_4; out of 1,000 simulation runs) as a function of sample size.

Sample size	Average ($HR_{i,j}$, $HR_{j,i}$)	Average ($PHR_{i,j}$, $PHR_{j,i}$)	VI	BA	UDOI
40	58	82	93	89	92
150	75	97	99.7	99.7	99.7
500	96	99.9	1	1	1

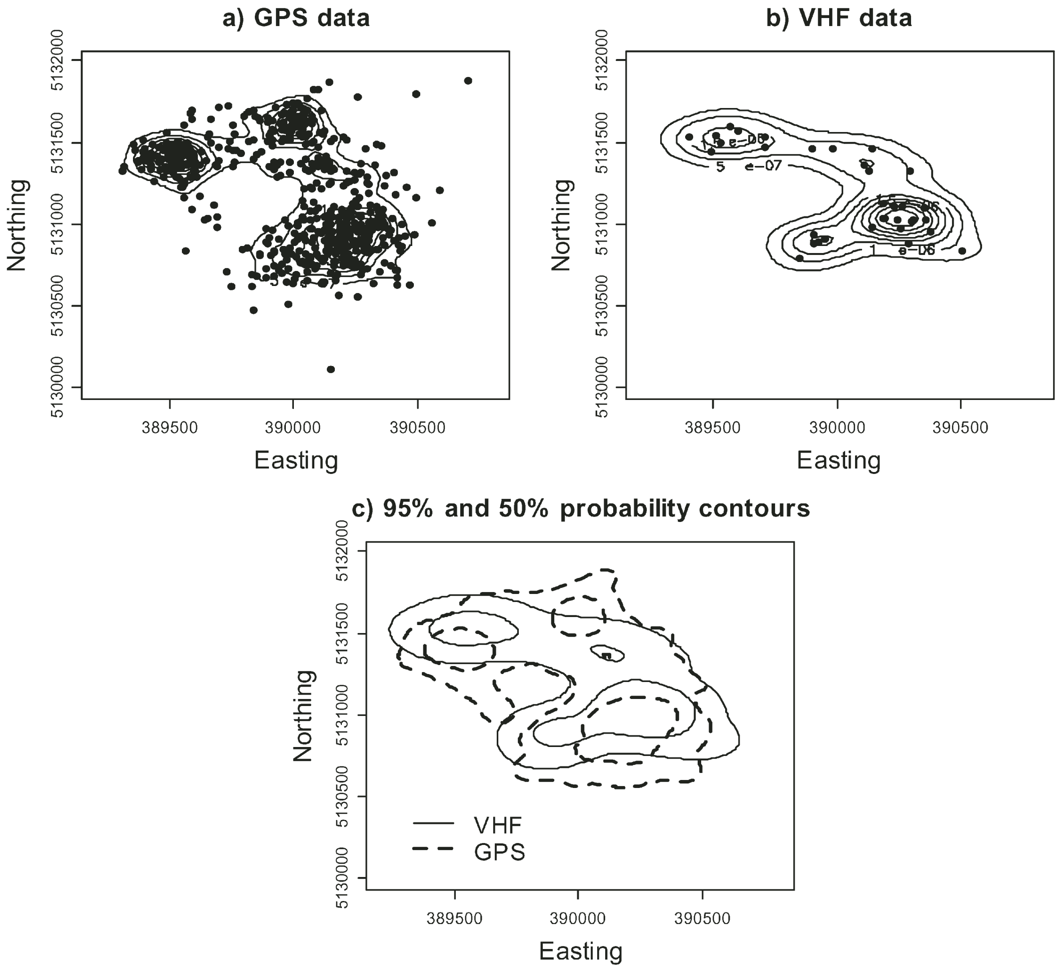

Fig. 4. Global Positioning System (GPS) and very high frequency (VHF) radiotelemetry locations for an adult female white-tailed deer in north-central Minnesota: (a) GPS data (n = 576) and associated contours of UD_{GPS}; (b) VHF radiotelemetry data (n = 34) and estimated contours of UD_{VHF}; and (c) 50% and 95% contours of the estimated utilization distributions (UDs) for the data in (a) and (b). Estimates of the UD were obtained using kernel density estimators with different smoothing parameters in the x and y directions chosen using the plug-in method (Sheather and Jones 1991).

We conducted triangulation on each deer from at least 3 known receiving stations and determined Universal Transverse Mercator (UTM) coordinates for receiver locations using hand-held Garmin 12-channel GPS receivers (GPS 12 Personal Navigator, GARMIN Corporation, Olathe, Kansas, USA). Receiving stations were assigned a unique number and description. Deer location estimates were derived by taking 3–7 simultaneous bearings using a 3-element folding Yagi antenna, radio receiver, and hand-held compass. We used a laptop computer programmed with XYLOG (Dodge and Steiner 1986) to immediately evaluate bearings, location estimates, and corresponding error ellipses in the field. Radio-locations were discarded if associated error ellipses were >6.0 ha (the average vegetation patch size at Camp Ripley). We calculated standard deviation of bearing errors using methods described by White and Garrott (1990) and used a standard group observer deviation of 8° in calculating the location estimate and error ellipse in XYLOG. Deer were primarily located during daylight hours (0700–1800), but 2–3 nocturnal (1900–0600) locations were estimated as well (we later censored these observations from our analysis). We located deer by triangulation 3–7 times per week from capture (late Jan–early Feb) to 31 March 1999 and 2000.

For the example illustrated below, we used 576 (84% fix success rate) and 34 diurnal locations for GPS and VHF data sets, respectively, for a single individual (Fig. 4a,b). The representative data set was part of a larger study comparing 14 paired GPS and VHF locations for adult female northern white-tailed deer on winter range in the Transition Zone in north central Minnesota (C. Kochanny, Department of Fisheries, Wildlife, and Conservation Biology; unpublished data). We used the same methods as for the simulation study to estimate the overlap indices; however, we used a grid cell size of 101 × 101. Estimates of home-range size using the 95% probability contour were similar for the 2 data sets (VHF 95% home range = 82 ha, GPS 95% home range = 97 ha). The shape of the home ranges, particularly the 50% core areas, differed slightly (Fig. 4). The GPS data indicated a high use area centered at roughly UTM Easting = 390,000, Northing = 5,131,600 that was not captured in the VHF data set. All of the overlap statistics were high ($HR_{GPS,\ VHF} = 0.71$, $HR_{VHF,\ GPS} = 0.84$, $PHR_{GPS,\ VHF} = 0.93$, $PHR_{VHF,\ GPS} = 0.80$, VI = 0.59, BA = 0.80, and UDOI = 0.88), suggesting the 2 conditional 95% UDs were quite similar (as we might expect since we took the observations from the same individual, and we believe the telemetry data were of high quality). Whereas the UDOI is not limited to the [0,1] interval, the other overlap measures are so constrained, and thus offered interesting comparisons. The averages of the 2 *HR* statistics and *PHR* statistics were 0.77 and 0.86, and BA = 0.8. By contrast, VI was only 0.59, seemingly suggesting less overlap than these other measures.

There were also some noteworthy comparisons between the area-based and the probability-based measures of overlap, $HR_{i,j}$ and $PHR_{i,j}$, respectively. The VHF-estimated 95% home range was slightly smaller than the corresponding GPS-estimated home range (Fig. 4c); therefore, the area of overlap ($A_{GPS,VHF}$) constituted a larger proportion of the VHF home range. The area-based measures reflected this fact with $HR_{GPS,\ VHF} = 0.71$ and $HR_{VHF,\ GPS} = 0.84$. Thus, 84% of the VHF-estimated home range was overlapped by the GPS-estimated home range, while 71% of the (larger) GPS-estimated home range was overlapped by the VHF-estimated home range. By comparison, the probabilistic measures were suggestive of a slightly higher degree of overlap ($PHR_{GPS,\ VHF} = 0.93$ and $PHR_{VHF,\ GPS} = 0.80$) and were of the opposite direction ($HR_{VHF,\ GPS} > HR_{GPS,\ VHF}$, whereas $PHR_{VHF,\ GPS} < PHR_{GPS,\ VHF}$). A potential advantage of the probability-based measures of overlap is that they were fairly easy to interpret. For example, these measures suggest that if one were to randomly generate location data using $\hat{UD}_{VHR,\ 0.95}$, 93% of these points would be expected to fall within the GPS-estimated 95% home range, whereas 80% of points randomly generated using $\hat{UD}_{GPS,\ 0.95}$ would be expected to fall within the VHF-estimated 95% home range.

DISCUSSION

Increased interest in quantifying overlap between home ranges for different animals or the same animal over time is likely due, in part, to newly developed UD-based estimates of home range (e.g., using kernel-density estimators), as well as to increased interest in spatial analyses facilitated by the widespread availability of Geographic Information Systems and software for analyzing spatial data. A few different indices have been suggested for quantifying the degree of static interaction or overlap in home-range estimates, with VI receiving the most attention in recent applications (Millspaugh et al. 2000, Marzluff et al. 2001, Roloff et al. 2001, Gitzen and Millspaugh 2003). Millspaugh et al. (2004) compared 2 area-based measures of overlap with VI to determine the extent to which the indices gave similar results across a range of simulated data (random vs. clumped data, more or less overlap). We ask perhaps a more fundamental question, which index provides the most reliable measure of space-use sharing or UD similarity?

Hurlbert (1978) argued that any index used to quantify overlap should be appropriate (i.e., it should produce measures consistent with one's intuition of overlap) and simple (i.e., easy to interpret). We tested the appropriateness of several indices of static interaction by examining their ability to accurately rank pairs of home-range estimates in terms of the degree of overlap. These tests suggest that the UDOI is likely to be the most appropriate index for quantifying overlap in terms of space-use sharing, while the BA statistic is likely to be most appropriate for quantifying the degree of similarity among UD estimates. In addition, the probabilistic measures, $PHR_{i,j}$, provide easily interpretable measures of overlap, and therefore they may be useful to report in conjunction with the other UD-based indices (BA, VI, UDOI). Because $PHR_{i,j}$ and $PHR_{j,i}$ account for differences in the relative probability of space-use through the estimated UDs, they are more appropriate than the area-based measures of overlap ($HR_{i,j}$).

Considerable caution should be applied when interpreting or comparing measures of overlap across studies. Estimates of overlap will almost always be biased too low for UDs with a high degree of overlap, and in some cases, too high if the UDs have little overlap. More importantly, the extent of the bias appears to depend strongly on sample size, suggesting that comparisons across studies may be problematic if they vary widely in sample size. These statements hold true for all of the overlap indices that we considered. We hesitate to generalize our conclusions based on the 1 simulation study we considered—particularly since the bias in the overlap statistics appeared to depend on the 2 UDs being compared and may depend on other factors not varied in the current simulation study (e.g., choice of UD estimator or choice of smoothing parameter if a kernel density estimator is used to estimate the UD). However, Seidel (1992) also noted similar biases with respect to sample size and degree of overlap in her simulation study. With the above concerns in mind, we argue that the indices still have merit as measures of space-use sharing or UD similarity. For example, it seems reasonable to infer a high degree of overlap for large sample values (e.g., >0.6 as in the GPS-VHF application that we presented). Furthermore, the ability of these indices to accurately rank pairs of UDs in terms of their overlap supports their recent application as meaningful response variables for correlation/regression analysis (Millspaugh et al. 2000, Roloff et al. 2001), as measures of site fidelity that can be compared across various time periods (Marzluff et al. 2001), and as reliability measures of various UD estimators (Gitzen and Millspaugh 2003).

Yet, application of these statistics may remain somewhat limited because it is difficult to determine appropriate confidence limits for their true measures. This problem also plagues nonparametric estimates of UDs and home-range estimators in general. Worton (1995) and Kernohan et al. (2001) suggested using the bootstrap to develop confidence bounds for UD-based estimates of home range, and Seidel (1992) suggested a similar approach for the overlap statistics themselves. However, estimating confidence limits using the bootstrap is problematic for kernel density estimators since they themselves are biased estimators, and it is not easy to estimate their bias (Davison and Hinkley 1997). We suggest that more work in this area would be useful if estimates of overlap are to be meaningfully compared across studies.

A few other caveats apply when choosing an index or method for quantifying overlap. We only considered static interaction analyses (i.e., analyses that ignore the temporal sequence of movement paths). A dynamic interaction analysis is likely to be more appropriate and informative when simultaneous measurements are available for different animals (see Kernohan et al. 2001 for a review of methods). In addition, the indices we presented assume availability of a fairly accurate and precise estimate of each animal's UD. Suggested sample sizes required for obtaining a reasonable estimate of home-range size vary from 30 to 50 observations (Seaman et al. 1999) to 200 observations (Garton et al. 2001). Accurately estimating the full UD for an individual animal will likely require at least this much data. When sample sizes are small, a more direct comparison of the location data (e.g., using average distances between observations within and between the 2 sets of locations) may be more informative. In particular, one can compare centroids of the observations to test for location shifts (White and Garrot 1990) or use multiple response permutation procedures (MRPPs; Mielke and Berry 1982, Biondini et al. 1988) to test whether the 2 sets of observations come from the same distribution. Multiple response permutation procedure tests are typically formulated in terms of average distances between observations within and among samples. For the application we considered (comparing GPS and VHF estimates of the UD), MRPP tests are not appropriate, since the GPS data are sampled at a much higher rate and therefore are expected to be closer together (on average) when compared to the VHF locations. However, we expect GPS-based estimates of the UD to be unbiased, since a systematic sampling design (sampling approximately every hour) was applied. The overlap indices we presented provide an alternative approach to analyzing these data and should be more robust to differences in sampling rates for the 2 data sets.

MANAGEMENT IMPLICATIONS

Home-range overlap indices have several important applications to wildlife research and management. As a quantitative measure of space-use sharing, overlap indices are useful for assessing the degree of interaction among individuals as well as site fidelity for a particular individual. In addition, overlap measures may be used to measure the reliability of various home-range estimators (e.g., by comparing estimates of utilization distributions from simulated data to known values). The most appropriate index to use will depend on the research question as well as availability of software and type of home-range estimator (e.g., minimum convex polygons versus UD-based estimators). Area based measures, $HR_{i,j}$, may be useful for quantifying overlap between home ranges calculated using the minimum convex polygon method. However, we suggest that UD-based estimates of overlap (VI, BA, and UDOI) should be preferred based on theoretical grounds (i.e., their better discriminatory power in a set of paired examples) as well as our simulation results. In particular, we recommend BA and VI for quantifying the degree of similarity among UD estimates and UDOI for quantifying space-use sharing.

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APPENDIX 1. CALCULATION OF OVERLAP INDICES

Although various parametric and nonparametric methods have been developed to estimate an animal's UD, kernel-based estimators are currently the most popular method (e.g., see Kernohan et al. 2001 for a recent comparison of methods). Kernel density estimators (as well as most other nonparametric methods) provide estimates of the UD across a series of grid points that can then be used to estimate home ranges based on the pth probability contour, $A_{i,p}$, numerically (Worton 1995). For example, the home range defined by the 95% probability contour is estimated by: (1) approximating the total probability associated with each grid cell =

$$\iint_{\text{grid cell}} \mathrm{UD}(x,y)\,dxdy \text{ by } \hat{\mathrm{UD}}(x,\ y)\ \Delta x\Delta y$$

(where Δx and Δy give the length and width of the grid cell), (2) sorting the cells in descending order, and (3) including grid cells with the highest probability until the resulting total probability (summed over the grid cells) = 0.95. Similarly, we can use numerical integration to approximate the various overlap statistics. Before applying these methods, it is important to check the adequacy of the grid over which the UD's have been estimated by calculating:

$$\sum_{i=1}^{n}\sum_{j=1}^{m}\ \hat{\mathrm{UD}}_1(x_i, y_j)\Delta x\Delta y \text{ and} \sum_{i=1}^{n}\sum_{j=1}^{m}\ \hat{\mathrm{UD}}_2(x_i, y_j)\Delta x\Delta y$$

These summations should be close to 1 (e.g., to the first 2 decimal points) if the grid size adequately covers the spatial domain of the observations and if the grid is not too course (since probability distributions must integrate to 1). In theory, the estimated UD will be nonzero for any point in space if a Gaussian kernel is used (the Guassian distribution has support on the full $(-\infty, \infty)$ interval). However, in practice the estimated UD will typically drop to zero (to machine precision) rather quickly outside the range of observed locations. Grid cells with very small, but nonzero estimates of the UDs will have little impact on the estimates of $PHR_{i,j}$, VI, and BA. However, estimates of the area of overlap, and hence the estimates of $HR_{i,j}$ and UDOI, will be sensitive to small nonzero estimates of the UDs. Therefore, it will often be preferable to use a tolerance (e.g., 10^{-15}) when estimating the area of overlap (e.g., setting = 0 for values of < tolerance). Alternatively, one can limit inference to conditional UDs in eq (3) (e.g., calculating the overlap indices using $\mathrm{UD}_{i,0.95}$).