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Home Range and Habitat Analysis using Dynamic Time Geography

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ABSTRACT Wildlife home ranges continue to be a common spatial unit for modeling animal habitat selection. Telemetry data are increasing in spatial and temporal detail and new methods are being developed to incorporate fine resolution data into home range delineation. We extended a previously developed home range estimation technique that incorporates theory from time geography, the potential path area (PPA) home range, to allow the home range to be defined at multiple spatial scales depending on the observed rate of movement within the data. The benefits of this approach are demonstrated with a simulation study, which uses multi-state correlated random walks to represent dynamic movement phases to compare the modified PPA home range technique with a suite of other home range estimation methods (PPA home range, kernel density estimation, Brownian bridges, and dynamic Brownian bridges). We used a case study on caribou (*Rangifer tarandus*) movement from northern Canada to highlight the value of this approach for characterizing habitat conditions associated with wildlife habitat analysis. We used a simple habitat covariate, percent forest cover, to explore the potential for misleading habitat estimates when home ranges do not include potentially visited locations (omission area) or include areas not possibly visited (commission area). We highlight the advantages of the dynamic PPA home range in the context of quantifying omission and commission areas in other home range techniques. Finally, we provide our R code for calculating dynamic PPA home range estimates.

KEY WORDS caribou (*Rangifer tarandus*), commission area, correlated random walk, omission area, telemetry.

With continued development of spatial tracking technologies (e.g., global positioning system [GPS], Argos), unprecedented datasets are facilitating novel research on wildlife movement and behavior. These improvements have resulted in wildlife telemetry data with finer sampling intervals, over longer temporal extents, and with better spatial accuracy (Cagnacci et al. 2010). Improved spatial and temporal resolution of telemetry data have provided scientists the opportunity to conduct increasingly detailed analysis of animal movement and the potential to answer increasingly sophisticated questions regarding wildlife biology, behavior, and response to change (Patterson et al. 2008).

The home range continues to be a primary spatial unit for wildlife analysis and modeling (Beyer et al. 2010). The most oft-cited definition of a home range is the area to which an animal confines its normal movements (Burt 1943). However, a robust mathematical formulation of this definition is still absent, and the practical definition of a home range is dependent on the chosen method for estimating it (Fieberg and Börger 2012). Thus, there are many approaches for estimating wildlife home ranges, for example minimum convex polygons, kernel density estimation (Worton 1989), local convex hulls (Getz and Wilmers 2004), and Brownian bridges (Horne et al. 2007).

Home ranges are a useful summary unit for spatial analysis of wildlife movement because they explicitly relate to processes (such as territoriality, spatial memory, and habitat preference) associated with space-selection patterns in many wildlife species (Börger et al. 2008, Van Moorter et al. 2009). As a conservation tool, home ranges represent a useful spatial unit for management decision-making and analysis (Reynolds et al. 1992, Bull and Holthausen 1993, Linnell et al. 2001). Home ranges are commonly used in 2 areas of spatial analysis: to quantify differences in home range areas and to study habitat selection. Quantifying differences in home range areas, for example between sexes (Swihart and Slade 1989), or over time (Smulders et al. 2012) provides insight into wildlife movement processes associated with spatial selection and mobility. Habitat analysis using home ranges links spatial selection to underlying environmental covariates and habitat types being used by the individual.

Analyzing changes in home range estimates, or the habitat variables associated with them, is complicated by the presence of areas of omission and commission error. Omission and commission areas are defined, respectively, as habitat used by the animal that is excluded from the home range and habitat that is unused but included in the home range (Sanderson 1966). Similarly, Getz and Wilmers (2004) refer to Type I error as including invalid areas and Type II error as excluding valid areas in home range estimates. Home range estimation methods that reduce omission and commission areas, or methods that can be used to quantify these areas in existing methods, are necessary to improve wildlife home range studies. However making comparisons across home ranges is difficult with empirical data because there is no truth for comparison and each method places different assumptions on the data.

The potential path area (PPA; Long and Nelson 2012) approach takes an alternative view on home range estimation, one based on a time geographic view of individual movement (Hägerstrand 1970). Within the time geographic framework, movement opportunities are represented using a space-time prism, which is a 3-dimensional (space and time) volume that contains all potential movement paths between 2 known telemetry fix locations (Fig. 1). The space-time prism represents a useful measure for understanding the spatial-temporal constraints on individual movement opportunity (Kwan 1999) and for this reason is commonly referred to as the accessibility space (Kwan 1998). The PPA is the projection of the space-time prism onto the spatial plane, and represents a purely spatial measure of accessibility (Fig. 1). The PPA home range is calculated by recursively computing PPA ellipses for consecutive pairs of telemetry locations, which are then combined (using a spatial union) to estimate the home range (see Long and Nelson 2012). The PPA home range estimate focuses explicitly on the delineation of the accessibility space of the individual, which makes it a useful spatial unit for comparing across methods in the context of omission and commission areas.

The size and shape of the space-time prism, and thus the PPA home range estimate, depends on the time between locations and a mobility parameter v_{max}, which can be interpreted as a maximum travel velocity. In some cases, v_{max} may be known based on a fine understanding of organism biology. In most cases, v_{max} must be estimated from the telemetry data; for example Long and Nelson (2012) outline several statistical procedures that can be used to estimate v_{max}, which are derived from methods for estimating the upper bound of a distribution given a set of values. With the PPA approach, v_{max} is a global parameter applied to the entire telemetry dataset (i.e., all pairs of points). With organisms that exhibit highly variable mobility levels, PPA home range estimates will overestimate home range area for periods of lower mobility, leading to increased commission areas, a problem also encountered with other methods (e.g., from over-smoothing; Gitzen et al. 2006, Downs and Horner 2008). A dynamic v_{max} parameterization incorporating higher and lower mobility levels will reduce over-estimation of home range areas associated with low mobility phases, and reduce commission area.

Explicitly considering wildlife movement phases is one approach to reducing omission and commission areas (Kranstauber et al. 2012). Kernel and minimum convex polygon approaches, for instance, cannot include movement phases because they ignore the temporal component of telemetry data. Most wildlife species exhibit multiple movement phases, often linked to different behaviors, resulting in variation in patterns and scales of movement, as well as habitat selection. A number of robust statistical techniques currently exist that can be used to identify different movement phases within a telemetry dataset (e.g., latent models: Morales et al. 2004, Jonsen, Flemming and Myers 2005; change-point analysis: Gurarie et al. 2009). Within each phase, movement parameters should follow a similar pattern, whereas between phases movement parameters shift dramatically from, for example, low motion (resting) to high motion (migration) states. To reduce omission and commission areas, space-time variation associated with different movement phases may be useful for refining home range estimates, and subsequently, habitat selection studies.

We extended the PPA approach by dynamically modeling the mobility parameter (v_{max}) so that variation in mobility, based on observed movement phases is incorporated into home range estimation.

We call the extension the dynamic potential path area home range (dynPPA). Using simulated data and empirical caribou (*Rangifer tarandus*) telemetry data, we demonstrate how the dynPPA approach provides an alternative measure of animal space use and a useful comparison metric among existing home range techniques for quantifying omission and commission areas. Finally, we provide an R-based toolset for performing dynPPA analysis.

METHODS

Dynamic PPA Home Range (dynPPA)

We follow Long and Nelson's (2012) method of estimating v_{max} from a telemetry dataset of n fix locations for a single individual. Estimates of v_{max} are a function of the distribution of individual segment velocities (v_i) given by:

$$v_i = \frac{d_i}{t_i} \quad [1]$$

where d_i is the distance and t_i the time between consecutive fixes. Based on the distribution of the v_i for the entire trajectory, v_{max} is an upper bound on the v_i, which can be estimated by several statistical estimation techniques (e.g., Robson and Whitlock 1964, van der Watt 1980). For example Long and Nelson (2012) suggest the method described by van der Watt (1980) which considers the ordered set of the v_i such that $v_1 < v_2 < \ldots < v_{m-1} < v_m$ and $m = n - 1$.

$$v_{\max} = \left(\frac{k+2}{k+1}\right) v_m - \left(\frac{1}{k+1}\right) v_{m-k} \quad [2]$$

where $1 < k < m$ represents the kth ordered value of v_i. We extend the v_{max} estimation procedure from Long and Nelson (2012) to account for behavioral shifts throughout the tracking period. Thus, dynamic v_{max} is defined by a similar function:

$$v_{\max,\,p} = F\left(v_{i,p}\right) \quad [3]$$

Where $v_{max,p}$ is the v_{max} estimate for the pth dynamic phase comprising of a subset of the n telemetry fixes and $F(v_{i,\,p})$ is a statistical technique (e.g., [2]) for estimating the upper-bound of a distribution applied to the v_i in phase p. The phases (p) may be from a temporally dynamic moving window, or associated with discrete behavioral phases. Although we used the technique described in van der Watt (1980), this approach can be used with other functions for estimating the upper-bound of a distribution. Importantly, such a dynamic calculation of the PPA (dynPPA) home range estimate allows for variations in the v_{max} parameter through time resulting from changes in movement behavior.

The construction of the dynPPA home range explicitly considers the movement ability of the individual animal to delineate their accessibility space throughout the movement trajectory. Thus, by taking a spatial overlay of the dynPPA and other home range estimators, we define areas included in the dynPPA home range but not included in home range estimates from other methods as omission area (Fig. 2); these are areas that were accessible to the animal but not included in the home range estimates from the other methods. Omission area is prevalent in most methods, and is included in the commonly accepted definition of a home range (i.e., the occasional sallies described by Burt 1943). Quantifying commission area is not as straightforward, because all home range estimates are likely to include locations not actually visited by the animal because of the incomplete nature of telemetry data. We define areas included in the home range estimates from other methods but not included in the dynPPA home range as observable-commission areas, which represent areas included in the home range but outside of the accessibility space of the animal (Fig. 2). Observable-commission areas represent locations the animal could not possibly have visited given the known fix locations and an upper-bound on mobility (v_{max}). For example, the presence of high-levels of observable-commission area is one of the main reasons why minimum convex polygons are problematic with irregularly shaped patterns of animal telemetry data (Harris et al. 1990, Barg et al. 2004). Through the analysis of these spatial differences, we show how the dynPPA home range method improves upon the original PPA model and provides a unique and complementary view to home range estimation by explicitly delineating the accessibility space of an individual animal. The dynPPA approach improves upon the PPA approach by accounting for changes in mobility relating to dynamic movement behavior. Further, dynPPA home range can be used to evaluate and refine home range estimates from other methods through the quantification of spatial differences, which we define as omission and observable-commission areas.

Other Home Range Methods

Many methods exist for computing wildlife home ranges; we focus on comparing the original PPA method, 3 more popular current approaches – kernel density estimation (KDE; Worton 1989), Brownian bridges (BB; Horne et al. 2007), and dynamic Brownian bridges (dynBB; Kranstauber et al. 2012) – and the new dynPPA approach. With KDE, BB, and dynBB, the home range is a 2-dimensional projection of the utilization distribution of the animal from which a percent volume contour is extracted to delineate home range as a polygon. Kernel density estimation relies on the selection of a suitable kernel bandwidth, which remains a highly contentious issue in home range analysis (Hemson et al. 2005, Fieberg 2007). The Brownian bridge approach models movement as a Brownian diffusion process anchored on 2 consecutive fixes. The n-1 Brownian bridges are combined to produce the BB home range, and in this sense it is comparable to the PPA approach. The BB home range requires the selection of 2 variance parameters, one related to uncertainty in fix locations, and the other termed the Brownian motion variance, which is related to the mobility of the animal. The Brownian motion variance parameter is estimated globally from the entire telemetry dataset (of an individual) using a leave-one-out estimation process (Horne et al. 2007). To generalize the BB approach, Kranstauber et al. (2012) developed the dynBB, which uses a temporally varying estimate of the Brownian motion parameter to account for dynamic movement phases.

Simulation Study

We simulated 1,000 correlated random walks (CRW) to compare home range estimation techniques. Correlated random walks rely on 2 parameters. The first (r) governs the level of serial correlation in turning angles and the second (h) is a scaling factor for the step-length distribution. To simulate dynamic movement behavior, we varied the number of distinct movement phases (*p*) within each simulated CRW between 5 and 10. For each movement phase, CRW parameters were chosen randomly but restricted in such a way that higher mobility phases (h = 3 to 5) were associated with more directed (i.e., correlated) movements (r = 0.3 to 0.7), and lower mobility phases (h = 1 to 3) were associated with more random movements (r = 0 to 0.4).

For each simulated CRW, we computed the potential path area home range (PPA), the 95% volume contour kernel density home range estimate, the 99% volume contour Brownian bridge home range, the 99% volume contour dynamic Brownian bridge home range, and the dynamic PPA home range. We computed kernel bandwidth for KDE using the half the reference bandwidth, a modification that can reduce the effect of over-smoothing in KDE when data exhibits clumpy patterns (Worton 1995). We selected the 95% volume contour because it is the most commonly chosen level in past home range studies (Laver and Kelly 2008) and is typically used to estimate the home range, whereas lower values (e.g., 50%) are used to delineate core area. We computed the variance parameter for the BB and dynBB models using the maximum likelihood method outlined by Horne et al. (2007) and assumed the error parameter to be appropriately small. We chose a 99% volume contour level for the BB and dynBB methods following Horne et al. (2007).

For each technique, we computed the home range area, plus the intersection area with the dynPPA to examine spatial differences among methods. Results from the simulated study are presented as percentages of the dynPPA for comparison purposes, thus making the area of the dynPPA home range estimate the baseline areal measurement.

Case Study – Caribou in Northern British Columbia, Canada

To further demonstrate the dynPPA approach, we used a dataset of the movements of 4 caribou over the course of a year (2001). The telemetry data were collected with a regular, 4-hour sampling interval, with < 5% fixes missing. Unlike the simulation examples, in telemetry studies the number and duration of movement phases are generally unknown. We use the behavioral change point algorithm (BCPA: Gurarie et al. 2009) to identify different movement phases for each individual caribou. The BCPA requires 2 parameters. The first is the BCPA search window (w; Gurarie et al. [2009] suggest $w > 30$); we used $w = 43$, approximately a 1-week interval in this example. The second parameter is a threshold that identifies significant change points; we used 21, which is half of w, similar to that used by Gurarie et al. (2009). We then computed the PPA, KDE, BB, dynBB, and dynPPA home ranges following the methods for parameter estimation outlined in the simulation study. We again explore the presence of omission and observable-commission area in various home range techniques in the caribou example through area overlap comparisons with dynPPA.

We estimated the habitat composition (i.e., land cover) for each home range based on each home range estimation method to examine the effect of method on the composition estimates. To represent land cover, we used the Canada's Earth Observation for Sustainable Development (EOSD) dataset (Wulder et al. 2008), which was derived from Landsat satellite imagery. We selected percent forest cover as an indicator of habitat because wooded areas are a primary habitat type for caribou, especially outside of summer months (Wood 1994, Seip 1998). We focus on the percent forest cover within each home range along with the sub-areas of the home range delineated as omission area and observable-commission area to examine whether the composition of these sub-areas differed from the overall home range, resulting in misleading composition estimates from home range methods.

RESULTS

Simulation Study

Our simulations revealed differences between estimated home range areas and the presence of omission and observable-commission area across different home range methods (Fig. 3). The PPA approach produced larger estimated home range sizes, as expected, whereas the BB and dynBB methods produced smaller home range estimates than dynPPA. Kernel density estimation produced home range estimates that could be either larger or smaller than dynPPA (Fig. 3). Omission area was greatest in the BB and dynBB methods, but this is expected because these methods produced the smallest home range estimates. In many situations, KDE also produced a substantial level of omission area, which is surprising given that in general KDE produced the largest home range size estimates. As expected based on definitions, omission area in the PPA was 0 because the PPA home range contains the dynPPA home range.

In all simulations, PPA and KDE produced an observable-commission area (Fig. 3). Of these, 790/1,000 of the simulation PPA home ranges and 975/1,000 of the simulation KDE home ranges contained observable-commission area comprising greater than 10.0% of the estimated home range. The average percentage of observable-commission area was highest in KDE at 36.2%, with an average of 14.6% for PPA. The BB and dynBB methods also produced some level of observable-commission area in nearly all simulations (998/1,000 and 997/1,000 simulations, respectively). However, neither method produced a simulation where the amount of observable-commission area was greater than 10% proportionally of the home range area. The average observable-commission area was small in BB and dynBB (1.2% and 0.7%, respectively). Overall, BB and dynBB compare best with dynPPA, likely owing to similar derivations based on the sequence of telemetry fixes (path-based), producing similar sizes and minimizing observable-commission area.

Case Study – Caribou in Northern British Columbia, Canada

The 4 caribou in northern British Columbia, whose data we analyzed, exhibited similar movement patterns consisting of 2 spatially disjoint seasonal ranges connected via movement corridors (Fig. 4). Estimated home range areas had similar patterns as seen in the simulation study, with larger estimated home ranges from the PPA and KDE methods, and smaller estimated home ranges from the BB and dynBB methods (Fig. 4). Kernel density estimation produced the largest estimated home ranges but also produced estimates that differed in shape and structure from the path-based methods.

With the caribou dataset, the trend in estimated home range areas showed PPA or KDE being largest, followed by dynPPA, BB, and dynBB (Fig. 5). In the case of caribou C4, the KDE home range estimate was much larger owing to difficulty in specifying a suitable bandwidth using the objective method chosen. The dynBB and BB methods are excellent at minimizing observable-commission areas, and produce estimated home range sizes similar to each other. The KDE and PPA approaches both produced substantial areas of observable-commission area, which is problematic in home range studies because these areas are outside of the defined accessibility space of the animal.

Estimated habitat composition revealed the potentially misleading effect of observable-commission areas (Fig. 6). For example, with the KDE method with data from caribou C2, the observable-commission area was a substantial portion of the estimated home range, and the percent forest cover was relatively high for this area. The high percent forest cover in the observable commission area portion of the home range in C2 resulted in the highest observed percent forest cover of all the home range methods, noticeably higher than any other estimates (Fig. 6). Conversely, in caribou C4, the percent forest cover was similar in the observable-commission area to that of the dynPPA home range, in this case leading to equivalent measures of percent forest cover, despite the substantial overlap of home range size by the KDE method. The BB and dynBB methods produced relatively small areas of observable-commission area, despite having substantial differences in percent forest cover between the home range and observable-commission areas. However, in caribou C3, estimates for percent forest cover were lower for the BB and dynBB methods because the omission area had a higher percent forest cover, which shows the potentially misleading effect of omission area.

DISCUSSION

Concepts from time geography can be used to explicitly consider the elapsed time between telemetry fixes, allowing home range estimation to use a path-based data representation (Long and Nelson 2012). Traditionally, home range estimation techniques borrowed from computational geometry or statistics, are point-based approaches, and define an enclosure or smooth a set of telemetry fixes. Point-based methods use only the spatial geometry of telemetry fixes and thus may be hindered by the serially correlated structure of modern telemetry datasets (Dray et al. 2010). Path-based methods for estimating the home range leverage the temporal structure inherent in telemetry datasets. For example, methods may consider consecutive telemetry fixes as anchor points in a diffusion (Brownian bridge) or diffusion-drift process (biased random bridge; Benhamou 2011). The Brownian bridge and biased random bridge methods delineate the utilization distribution of an individual based on random walk theory, whereas the dynPPA home range method focuses on quantifying the polygon area accessible to an individual given *n* telemetry fixes and a time-varying mobility parameter.

The dynPPA method takes an alternative view on estimating the home range, one that explicitly considers that accessibility can be used to directly estimate the home range. That is, the dynPPA delineates the area an animal could have visited based on a set of telemetry fixes and a time varying mobility parameter v_{max}. We have demonstrated that dynPPA home range estimates can provide useful stand-alone measures for estimating home range areas, comparable with popular existing methods. We highlight the dynPPA approach as being simple and intuitive, but also stress how it can be used to identify omission and observable-commission areas when comparing across multiple methods, a practice increasingly common given the ease at which multiple methods can be implemented within a single software (e.g., Calenge 2006). Specifically, because the dynPPA home range estimate focuses on accessibility in its definition, we demonstrate how dynPPA can be used to quantify omission and observable-commission area in other estimation techniques. Such comparisons are conditional on the predication that the dynPPA estimate, which defines the individual accessibility space, represents a suitable baseline for identifying omission and observable-commission area.

Wildlife researchers now have an array of computational tools from which to choose for carrying out sophisticated spatial-temporal analyses on wildlife telemetry datasets. However, there remains a need to define relatively straightforward spatial analysis units, drawing on the foundational concept of the home range. The dynPPA home range method is based on different assumptions from other home range approaches. We propose that because dynPPA explicitly considers accessibility in its definition, it can be used for quantifying omission and observable-commission areas through direct spatial comparisons of home range polygons. Further, many studies are interested in studying habitat use versus habitat availability from telemetry data (Beyer et al. 2010). In use versus availability study designs, the researcher must carefully consider how they define available habitat. At some scales, a home range estimate (or a spatial extension of the home range such as a buffer around the home range) is used to define potentially available habitat (Long et al. 2010). A time geographic approach (i.e., dynPPA) is a logical method for identifying what constitutes available habitat in use versus availability studies because dynPPA explicitly delineates accessible areas.

Our simulation study highlights the challenges with home range analyses that researchers have been grappling with for decades: that different home range methods can lead to highly variable estimates of home range size and configuration. When compared to other home range estimation methods, dynPPA is generally larger than produced by BB or dynBB methods but smaller than for KDE and the original PPA approach. From comparisons between home range estimates from other methods with dynPPA, a researcher can decide whether a home range method is appropriate with a given dataset, or re-evaluate the chosen parameter combinations. Our simulations can also be seen as further evidence of the difficulty with KDE home range methods or more specifically the problem of automated selection of the bandwidth (Hemson et al. 2005). In the simulation study, we use a popular ad hoc method for identifying the kernel bandwidth (i.e., half the reference bandwidth), but the resulting home range estimates were highly variable in size. When the home range is overestimated, the result is substantial observable-commission area, which can be problematic when using home ranges for habitat composition analysis.

The results (both from the simulations and caribou study) confirmed that, like many home range estimation methods, the original PPA approach (Long and Nelson 2012) may be overestimating home range areas. We built on the ideas proposed by Kranstauber et al. (2012), that home range estimation methods should consider different movement phases associated with variable movement parameters. Thus, dynPPA is a generalization of the original PPA approach, where v_{max} is estimated independently for each movement phase. This approach considers movement phases as discrete segments along the trajectory, such that changes in movement parameters occur abruptly between phases (Kranstauber et al. 2012) and typically represent a change in movement behavior (e.g., migrating vs. foraging). Alternatively, movement parameters may vary continuously over time, and we have also implemented a temporal moving-window approach for estimating v_{max} dynamically over time. We did not evaluate the temporal moving-window method here but make it available with the R code provided to allow researchers to use a moving-window approach should it be appropriate with their research (see Supporting Information).

Methods for estimating movement parameters are complicated by missing fixes and irregular fix intervals (see Laube and Purves 2011), issues commonly encountered in empirical wildlife telemetry studies. Shorter than average fix intervals may be associated with higher segment velocities (v_i), which would be unrealistic with longer fix intervals. Many tracking devices are programmed to obtain fixes at specific intervals, which if they fail, continue to re-attempt fixes until successful. This can result in fixes that were programmed at regular intervals being collected at irregular intervals, some of which may be relatively short. If these short fix intervals are associated with a burst of movement, a relatively high v_{max} estimate will result, which will be inappropriate with longer intervals. Also, many modern telemetry studies are programming wildlife tracking devices to vary the tracking interval depending on time of day (e.g., 15-min tracking interval during the day and 2-hr interval at night). In such cases, estimates of v_{max} associated with the shorter interval would not reflect the estimates during the 2-hour period. Such discrepancies are due to the fact that animals are limited in their ability to maintain faster movement speeds over longer time intervals. When unrealistically high v_i values are included in the distribution of the v_i, it will become positively-skewed, and the v_{max} parameter will be overestimated. Overestimation of v_{max} results in a home range area that is unexpectedly large when using the dynPPA approach. A similar process occurs with other home range techniques, such as when the bandwidth (in kernel density estimation) or the variance parameter (in Brownian bridge models) is overestimated. When using the dynPPA home range method on wildlife datasets with irregular or missing fixes, the over-estimation of v_{max} can be reduced by examining the skewness of the v_i distribution and analyzing those segments above a chosen threshold independently. Long and Nelson (2012) suggested that the PPA approach was useful only with relatively dense and regularly sampled telemetry data. However, dynPPA is more suitable with irregular tracking schemes because the tracking interval can be directly related to movement phases (e.g., p in [3]) in the calculation of v_{max}. However, more research is needed to study the effect of variable and missing data on the v_{max} estimation procedure associated with dynPPA home range estimates.

Wildlife exhibit different movement phases associated with different movement behaviors (e.g., migration, foraging, searching). Distinct movement phases result in different movement patterns, and thus influence the patterns observed in telemetry data from wildlife tracking systems. Mathematical models for examining variations in animal movement behavior have become increasingly sophisticated and provide novel insights into fine-scale variations in animal behavior (Langrock et al. 2012, McClintock et al. 2012). However, methods incorporating dynamic behavior into analysis of wildlife space use (i.e., home range analysis) remain limited. The inclusion of changing behavior in wildlife movement models and spatial analysis is essential for improving space-use estimates (Kranstauber et al. 2012), and the subsequent analysis of underlying environmental variables. The dynPPA represents a new approach that can easily incorporate animal movement behavior phases, estimated via robust statistical models, directly into the home range estimation procedure.

Each technique for home range estimation is based on unique methods and assumptions and as a result is likely to produce different home range shapes and sizes (Fieberg and Börger 2012). Variation between methods has led many authors to compare across home range methods (Huck et al. 2008), often to highlight the deficiencies in existing approaches in specific scenarios (Downs and Horner 2008). The difficulty in selecting a method for home range estimation, especially with empirical data, is that there is no truth. Our comparisons, across 5 home range estimation methods, emphasize the unique information content of each method and how these approaches can be chosen based on research questions and the nature (i.e., resolution and extent) of the data from which the home range is to be estimated (Fieberg and Börger 2012, Powell and Mitchell 2012). When research questions emphasize accessibility (in space and time), dynPPA represents an appropriate home range estimator, given relatively high-resolution telemetry data. The concept of accessibility is useful when researchers wish to study whether animals have the potential to interact with features on the landscape (e.g., well sites, Sawyer et al. 2006, or roads, Long et al. 2010). With other research questions or data types, other home range estimation techniques may be more appropriate. For example, with coarse tracking data associated with satellite very high frequency (VHF) radio collars where serial correlation is lower, KDE methods are more appropriate. With animals that exhibit compact and regular shaped territories, simpler methods, such as minimum convex polygons, may be sufficient for estimating home range size and shape (Downs and Horner 2008). Further, when comparisons among multiple home range estimates are being made, in either an exploratory or analytical stage, we demonstrate the value of including the dynPPA method, where appropriate, because dynPPA can serve as a baseline from which to quantify omission and observable-commission area.

MANAGEMENT IMPLICATIONS

Home ranges are a typical spatial unit for conservation. The presence of omission and observable-commission areas in home range estimation and subsequent habitat analysis can be misleading. In an era of increasing geographical pressures on conservation activities, tools such as the dynPPA home range can assist in the conservation of wildlife by refining spatial estimates of home range. Simply, the dynPPA home range method can be used to assess if areas within a home range were accessible to an animal given spatial-temporal constraints. We provide some guidelines for conducting home range analysis using dynPPA and further demonstrate how to use dynPPA to investigate omission and observable-commission area in comparisons with other home range methods. Home ranges containing substantial omission or observable-commission areas should be used with caution because they may misrepresent the size of the home range, which can result in misleading habitat analyses. By carefully considering the presence of omission and observable-commission area in home range estimates, wildlife managers can improve the geographic focus of conservation efforts. Finally, we provide a free and open tool for computing the dynPPA, in the statistical software R, to make the calculation of dynPPA available to other researchers.

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FIGURE CAPTIONS

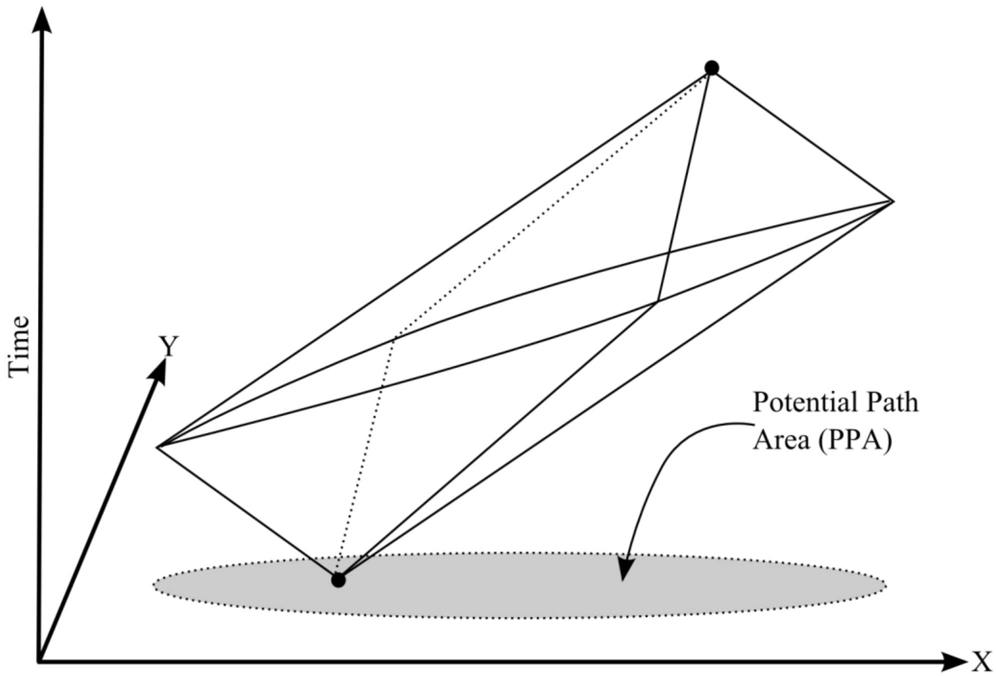

Figure 1. The space-time prism from time geography that delineates the accessibility space for movement between 2 constraint fixes, based on a known mobility parameter (v_{max}), which controls the size of the prism. The potential path area (PPA) is the projection of the space-time prism onto the spatial plane, and geometrically can be represented as an ellipse.

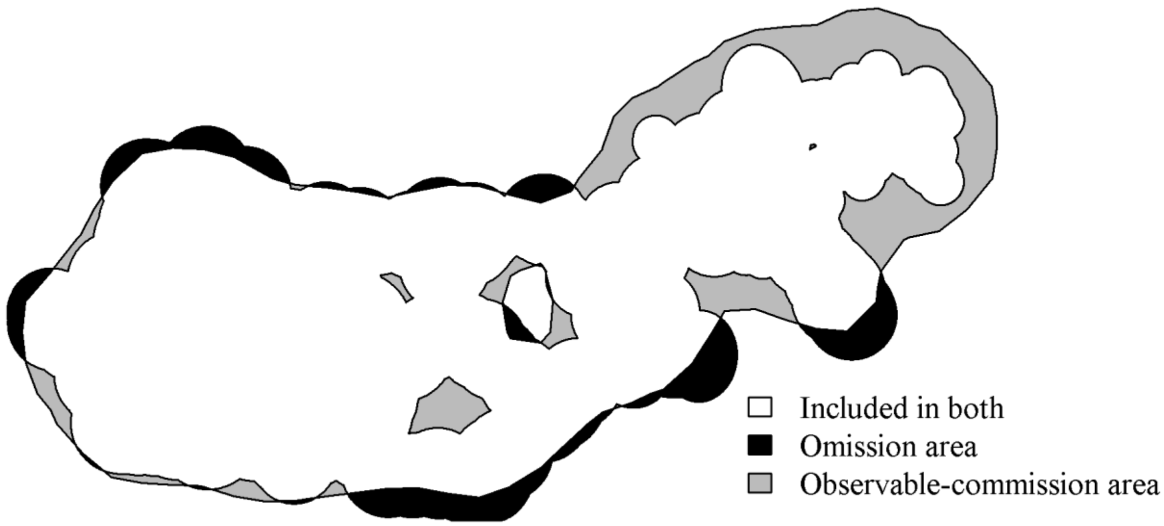

Figure 2. Comparison of a typical home range, with a dynamic potential path area (PPA) home range demonstrating how omission and observable-commission areas can be quantified and mapped.

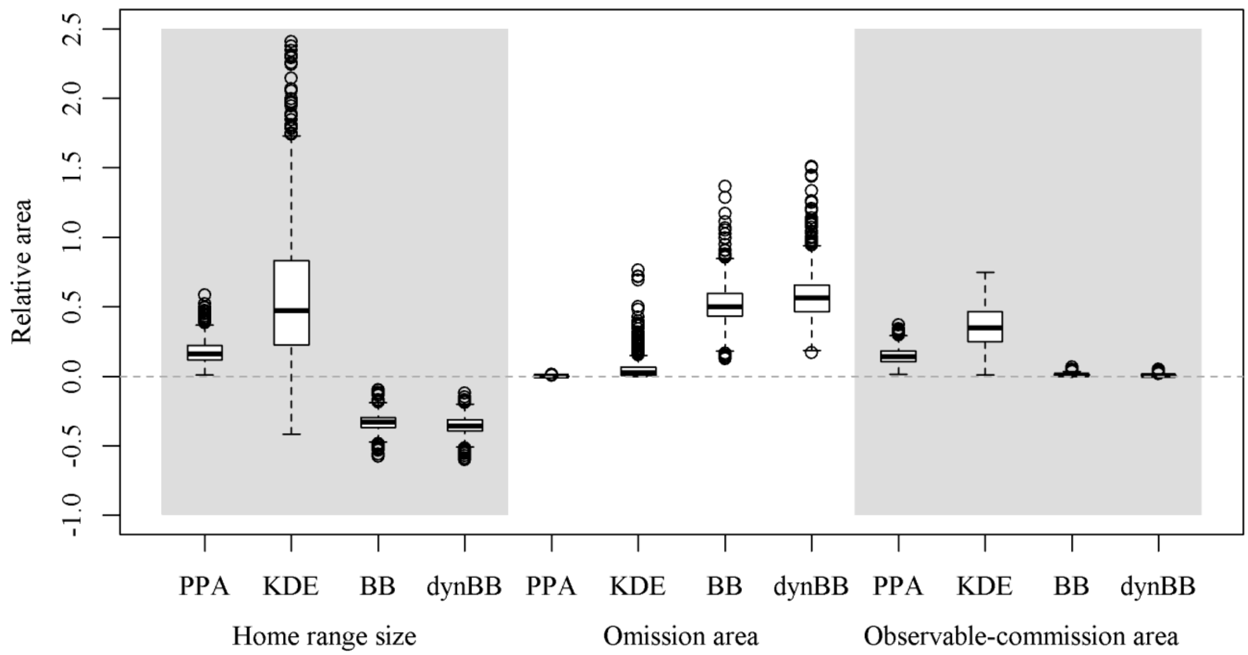

Figure 3. Boxplots showing the relative area of the potential path area (PPA), kernel density estimate (KDE), Brownian bridge (BB), and dynamic Brownian bridge (dynBB) home range estimation methods in comparison to the dynamic potential path area (dynPPA) method (panel 1), the amount of omission area in each method relative to the area of the individual home range (panel 2), and the amount of observable-commission area in each method relative to the area of the individual home range (panel 3). The median line is located within the boxes that delineate the interquartile range (25^{th} and 75^{th} percentiles) of the data. Whiskers extend to 1.5 the interquartile range, with outliers plotted as points.

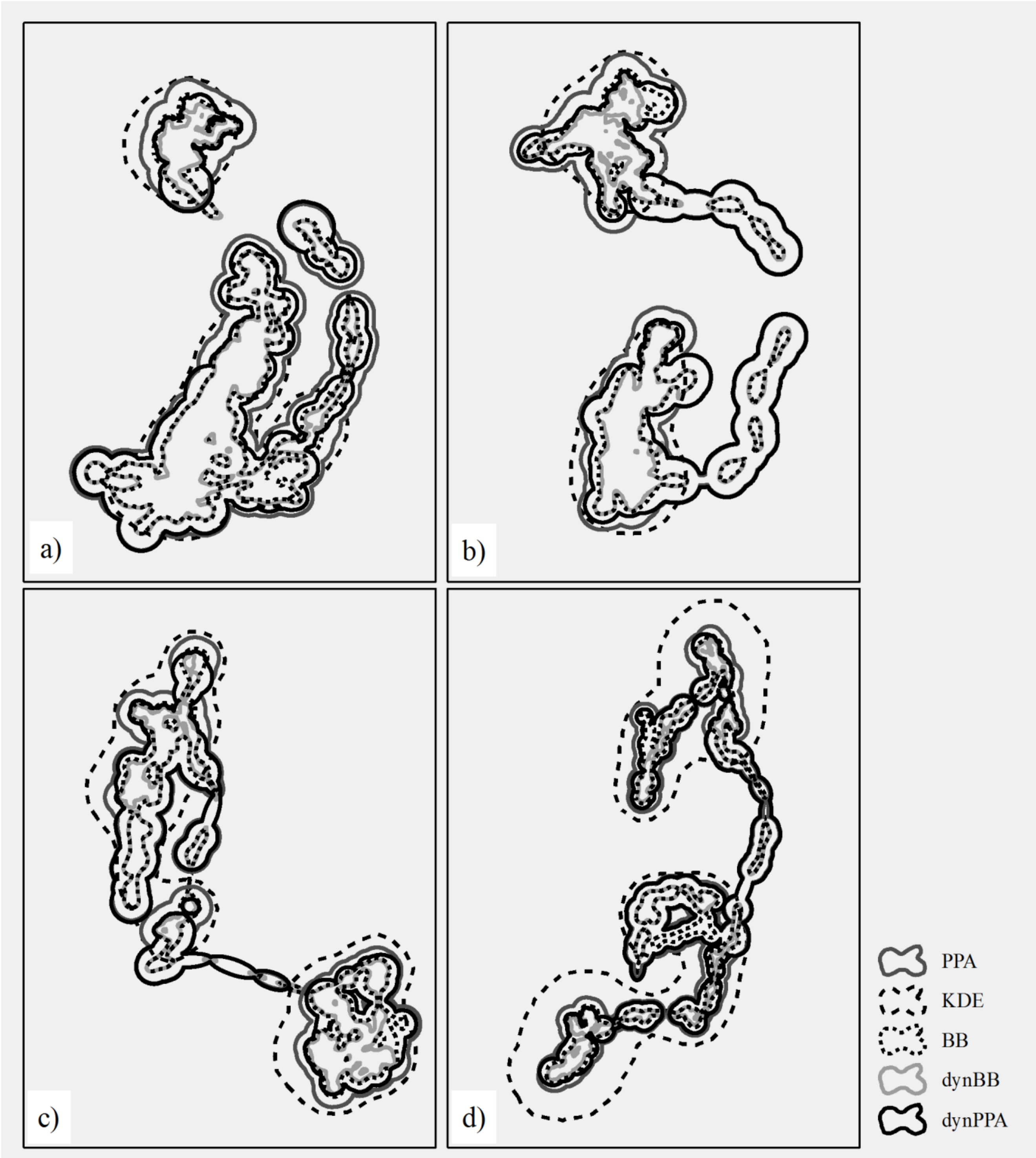

Figure 4. The potential path area (PPA), kernel density estimate (KDE), Brownian bridge (BB), and dynamic Brownian bridge (dynBB), and dynamic potential path area (dynPPA) home range estimates for each of 4 caribou: a) caribou C1, b) caribou C2, c) caribou C3, and d) caribou C4.

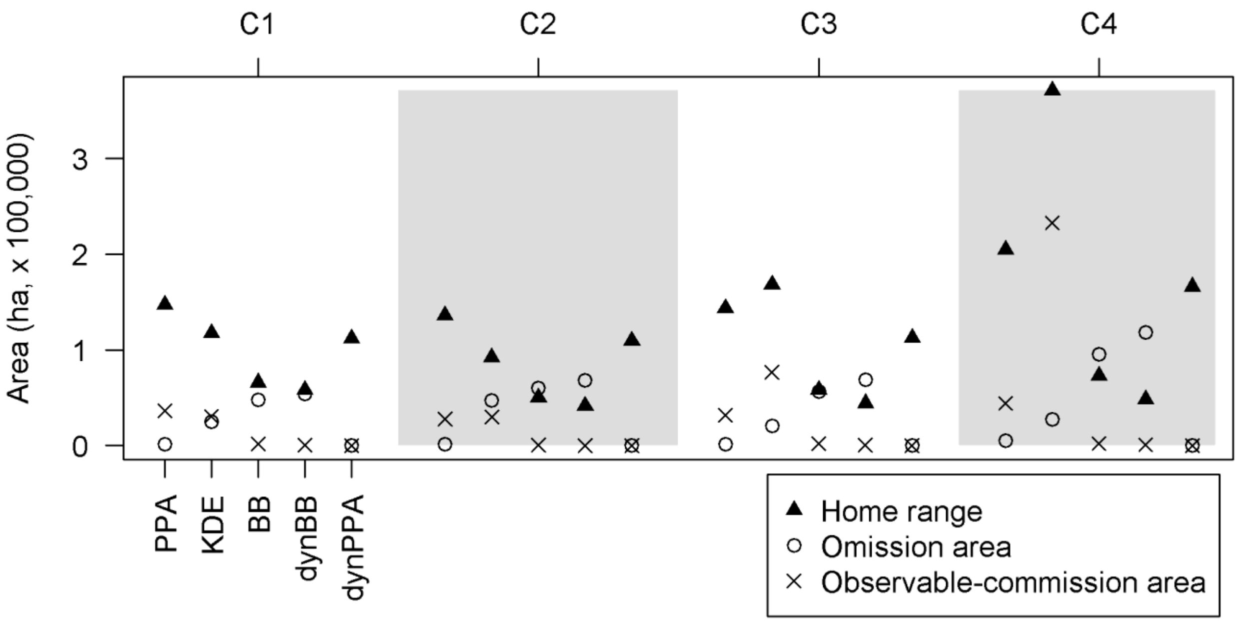

Figure 5. The potential path area (PPA), kernel density estimate (KDE), Brownian bridge (BB), and dynamic Brownian bridge (dynBB), and dynamic potential path area (dynPPA) home range areas for each of 4 caribou (C1, C2, C3, and C4) compared, along with the area of omission and observable-commission area for each home range method.

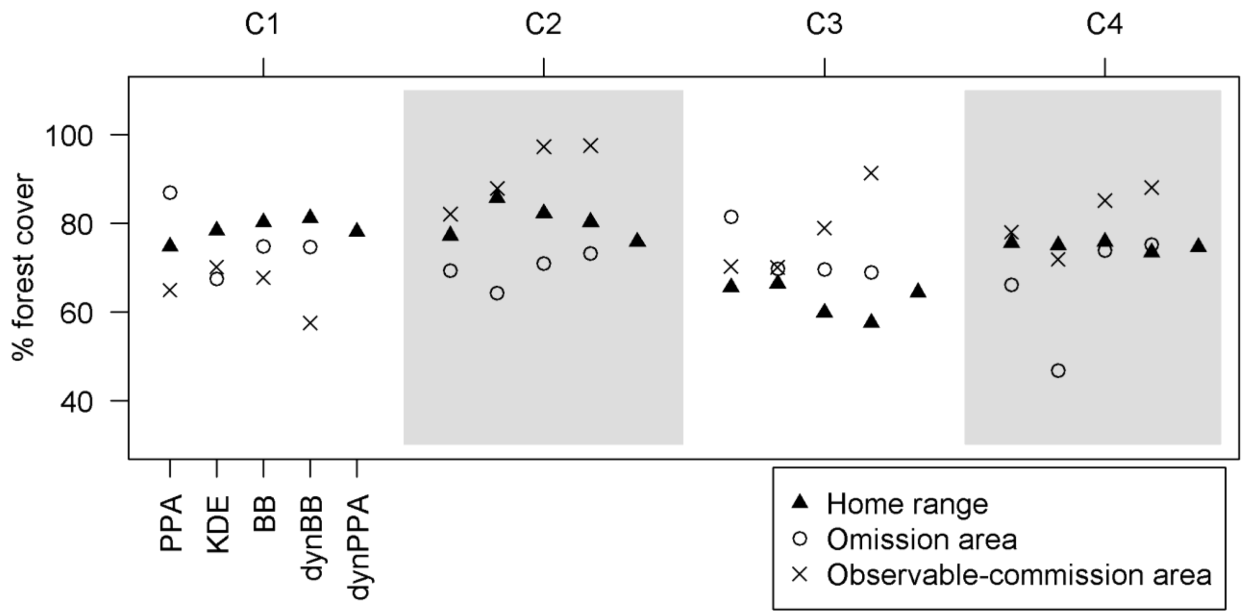

Figure 6. Percent forest cover within the potential path area (PPA), kernel density estimate (KDE), Brownian bridge (BB), and dynamic Brownian bridge (dynBB), and dynamic potential path area (dynPPA) home ranges for each of 4 caribou (C1, C2, C3, and C4), along with the percent forest cover within the omission and observable-commission areas within each home range.