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Tools and Technology

ctmmweb: A Graphical User Interface for Autocorrelation-Informed Home Range Estimation

JUSTIN M. CALABRESE,[1,2,3,4,5] *Center for Advanced Systems Understanding (CASUS), Untermarkt 20, 02826, Görlitz, Germany*
CHRISTEN H. FLEMING,[5] *Smithsonian Conservation Biology Institute, 1500 Remount Rd, Front Royal, VA 22630, USA*
MICHAEL J. NOONAN,[4] *The Irving K. Barber School of Arts and Sciences, The University of British Columbia, Okanagan campus, 1177 Research Road, Kelowna, BC V1V 1V7, Canada*
XIANGHUI DONG, *Department of Biology, University of Maryland, College Park, MD 20742, USA*

ABSTRACT Estimating animal home ranges is a primary purpose of collecting tracking data. Many widely used home range estimators, including conventional kernel density estimators, assume independently-sampled data. In stark contrast, modern animal tracking datasets are almost always strongly autocorrelated. The incongruence between estimator assumptions and empirical reality often leads to systematically underestimated home ranges. Autocorrelated kernel density estimation (AKDE) directly models the observed autocorrelation structure of tracking data during home range estimation, and has been shown to perform accurately across a broad range of tracking datasets. However, compared to conventional estimators, AKDE requires additional modeling steps and has heretofore only been accessible via the command-line ctmm R package. Here, we introduce ctmmweb, which provides a point-and-click graphical interface to ctmm and streamlines AKDE, its prerequisite autocorrelation modeling steps, and a number of additional movement analyses. We demonstrate ctmmweb's capabilities, including AKDE home range estimation and subsequent home range overlap analysis, on a dataset of four jaguars from the Brazilian Pantanal tracked between 2013 and 2015. We intend ctmmweb to open AKDE and related autocorrelation-explicit analyses to a wider audience of wildlife and conservation professionals. © 2021 The Authors. *Wildlife Society Bulletin* published by Wiley Periodicals LLC on behalf of The Wildlife Society.

KEY WORDS AKDE, animal movement, autocorrelation, ctmm, telemetry, tracking data.

Home range estimation ranks among the analyses most routinely applied to animal tracking data. Though many approaches to quantifying home ranges exist, kernel density estimators (KDE; Worton 1989) represent the most widely used class of home range estimation methods due to their flexibility, ease of use, and statistical efficiency (Laver and Kelly 2008). Historically, KDE have assumed independently sampled data (Laver and Kelly 2008), but in stark contrast, modern global-positioning system (GPS) tracking datasets are nearly always autocorrelated (Noonan et al. 2019; Noonan et al. 2020). Regardless of the means of locomotion (e.g., walking, hopping, flying, swimming, etc.), animals trace continuous paths through the environment (Turchin 1998). An unavoidable consequence of the continuity of animal movement paths is that finer sampling in time leads to more strongly autocorrelated tracking data (Swihart and Slade 1985). Global positioning system sampling rates have increased in lock step with technological advances, and it is becoming fairly common to speak of sampling rates in terms of hertz (observations per second; Kays et al. 2015, Noonan et al. 2015). Looking to the future, the strength of autocorrelation in tracking data will likely continue to increase as improvements in tracking technology facilitate the ever-finer sampling of animal paths.

There has been a long-running and inconclusive debate about how problematic autocorrelated data are for home range estimators that assume independently and identically distributed (IID) data (Swihart and Slade 1985, de Solla et al. 1999, Blundell et al. 2001, Fieberg 2007). Recent work based on a

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[1] *E-mail: j.calabrese@hzdr.de*
[2] *Helmholtz-Zentrum Dresden Rossendorf (HZDR)*
[3] *Helmholtz Centre for Environmental Research—UFZ, Department of Ecological Modelling, Permoserstr. 15, 04318 Leipzig, Germany*
[4] *Smithsonian Conservation Biology Institute, 1500 Remount Rd, Front Royal, VA 22630, USA*
[5] *Department of Biology, University of Maryland, College Park, MD 20742, USA*

large empirical dataset (369 individuals, 27 species, five continents) covering the full range of autocorrelation strengths has provided strong evidence that, when applied to autocorrelated data, IID home range estimators are negatively biased (Noonan et al. 2019). Furthermore, the magnitude of the bias increases in proportion to the strength of autocorrelation in the data (Noonan et al. 2019). Specifically, conventional KDE estimators that rely on the IID assumption underestimated home range areas by factors ranging from 2 to 13, depending on the bandwidth optimizer, with a similar degree of underestimation for geometric methods such as minimum convex polygons and local convex hulls (Noonan et al. 2019). One viable solution to the autocorrelation problem in home range estimation is to appropriately model the autocorrelation in the data as part of the home range analysis (Fleming et al. 2015). Doing so amounts to nothing more than ensuring that the assumptions made by the home range estimator are at least broadly similar to the major features in the data. Autocorrelated kernel density estimation (AKDE) home range estimation explicitly accounts for autocorrelation in the data by: 1) selecting the most appropriate autocorrelation model for the data via information theoretic methods, and 2) optimizing the smoothing bandwidth of the KDE based on the selected autocorrelation model (Fleming et al. 2015, Fleming and Calabrese 2017). In contrast to estimators that make the IID assumption, the large-scale comparative analysis of Noonan et al. (2019) showed, via block cross-validation performance (Roberts et al. 2017), that AKDE is consistently accurate across the full spectrum of sample sizes and autocorrelation strengths represented in their dataset.

Although the benefit of explicitly modeling autocorrelation in the data is improved accuracy (Fleming and Calabrese 2017, Winner et al. 2018, Noonan et al. 2019), the cost is greater analytical complexity and extra modeling steps that must be taken prior to home range estimation (Fleming et al. 2015, Calabrese et al. 2016, Fleming and Calabrese 2017, Fleming et al. 2019). Specifically, an appropriate model for the autocorrelation structure of the data must first be identified, and then used as a basis for AKDE home range estimation (Fleming et al. 2015). The R (R Core Team 2020) package ctmm implements these prerequisite modeling steps, as well as AKDE estimation and a suite of related analyses (Fleming and Calabrese 2015, Calabrese et al. 2016), but requires R programming knowledge. To make AKDE available to a broader audience, we introduce ctmmweb (Dong et al. 2018), which is an R Shiny-based (Chang et al. 2019) graphical user interface to the ctmm package, and includes additional functionality for publication-quality graphics, interactive maps, and reproducible research. We demonstrate the capabilities of ctmmweb, and its workflow for home range and overlap analysis, on an example featuring jaguars (*Panthera onca*) in the Brazilian Pantanal during 2013 to 2015 (Morato et al. 2018).

METHODS

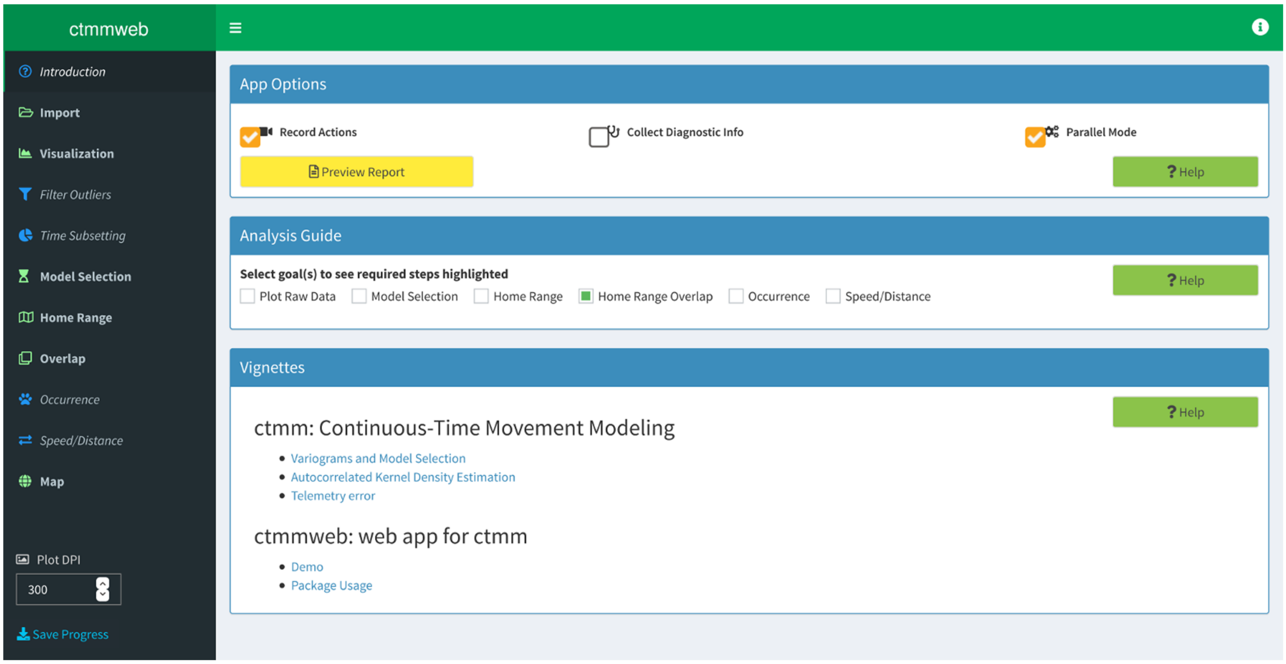
Although ctmmweb has a wide range of capabilities and can perform many types of movement analyses, in the current paper we detail only the steps necessary to reproduce the home range and overlap analysis. The app consists of a series of pages, with each page containing related functionality. For example, the Import page supports several different means of importing data into ctmmweb. Within each page, boxes are used to further separate different functions. Help buttons occur within boxes and provide guidance on the functionality contained in the focal box. The pages are indexed in ctmmweb's sidebar on the left side (Fig. 1), and a typical analysis proceeds by moving down the sidebar sequentially from one page to the next. Below, we discuss each page required to estimate the home ranges and overlap of four jaguars in the Brazilian Pantanal.

Introduction

The introduction page allows the user to configure certain app settings (e.g., whether or not to use multiple processor cores for parallelization), and provides guidance on how to use ctmmweb. To facilitate reproducible research, the Record Actions checkbox, which is checked by default, ensures that the app records all actions, datasets used, analyses, results, and figures. An archive of the user's ctmmweb session can be downloaded at any time (and from any page) by pressing the Save Progress button on the bottom of the sidebar. In addition to containing the aforementioned elements, the archive also provides a combined .html work report that can serve as a detailed description of the ctmmweb session. The Analysis Guide provides visual cues for the user to follow to accomplish an analysis goal or goals. The guide is off by default and requires the user to select a goal (or set of goals) from the listed checkboxes. The required steps to achieve a chosen goal, for example home range overlap analysis, are then shown with boldface type and a green icon in the sidebar (Fig. 1). The user then only needs to follow the highlighted steps sequentially from the top to the bottom of the sidebar to achieve their selected goal. Finally, a series of vignettes on ctmmweb and the analyses it supports are provide to give more detailed guidance.

Import

The app assumes that data are in Movebank.org format (Wikelski and Kays 2014), which is a tabular, .csv plain text format with one observation per row and columns that minimally include: individual.local.identifier (or tag.local.identifier), timestamp, location.long and location.lat. One can either manually create (e.g., in R or a spreadsheet program) an appropriately formatted .csv by including and correctly naming the above-listed elements, or use Movebank. For the latter option, one can either download a .csv from Movebank and manually import it into ctmmweb (via Upload Data), or use ctmmweb's Import from Movebank dialog to directly import the data into the app without requiring the data be stored locally. It is also possible to import a previously saved ctmmweb session archive via the Restore Progress dialog, so that the researcher can pick up where they left off, perform additional analyses and/or modify existing ones, and save the results in an updated archive. The jaguar data used in our paper can be imported by selecting jaguar from the list of built-in datasets and clicking load.



☑ Record Actions ☐ Collect Diagnostic Info ☑ Parallel Mode

Select goal(s) to see required steps highlighted

☐ Plot Raw Data ☐ Model Selection ☐ Home Range ☑ Home Range Overlap ☐ Occurrence ☐ Speed/Distance

ctmm: Continuous-Time Movement Modeling

- Variograms and Model Selection
- Autocorrelated Kernel Density Estimation
- Telemetry error

ctmmweb: web app for ctmm

- Demo
- Package Usage

Figure 1. The user interface of ctmmweb. The analysis workflow proceeds from page to page down the left-hand sidebar, though some pages may be skipped depending on analysis goals. The Introduction page is currently displayed, showing the Analysis Guide feature, which in this case, highlights the workflow steps necessary to complete home range overlap analysis.

Visualization

The imported individuals are listed in a table on the Visualization page, which provides descriptive statistics and a means for the user to select which individuals to include in the analyses. The selected individuals are then used throughout the rest of the app. A number of basic graphics are available on the Visualization page. For example, a scatterplot shows the raw (x, y) locations of all selected individuals together in the same panel, color coded by individual. In contrast, facet plots show the (x, y) locations of each individual in its own panel, with the same axis ranges used across all panels to facilitate comparison. All of the figures produced in the app will be saved to the session archive upon clicking Save Progress at the resolution indicated in the Plot DPI box immediately above the save button.

Model Selection

Variogram analysis, which is available on the Model Selection page, is the core visual diagnostic used to examine the autocorrelation structure of a tracking dataset (Fleming et al. 2014, Calabrese et al. 2016). Variograms depict the averaged squared displacement between all pairs of points separated by a given time lag (e.g., 1 hour), plotted as a function of time lag. Variograms allow one to visually assess, among other features, the appropriateness of home range analysis and the degree to which there is directional persistence in the movement. In the former case, an asymptote at larger time lags indicates evidence of range residency in the data, which implies home range analysis is appropriate. Conversely, the lack of a clear asymptote would indicate no evidence for range residency and would suggest that home range analysis is inappropriate for the focal dataset. While analyses other than home range estimation are still possible with non-range-resident data, ctmmweb does not currently support the non-range-resident movement models required in such cases; the user would instead have to turn to ctmm. Second, upward curvature on the short-lag end of the variogram is evidence of correlated velocity in the data, and suggests that a correlated velocity model would be appropriate (see model selection, below). Recalling that velocity consists of both movement speed and direction of travel, correlated velocity implies directional persistence in the movement. The app features rich functionality for variograms and by default produces a multi-panel display featuring a variogram for each individual in the dataset (Fig. 2). Superimposed on each variogram is an algorithmically-generated guess at initial parameter values for fitting a movement model to the data. If the visual correspondence between the empirical variogram and the guess is poor, the underlying parameter values can be manually adjusted for each individual via a dialog box with parameter sliders.

After visual examination of the data, clicking the Modeled tab on the Model Selection page performs automated model fitting and selection, based on the initial parameter value guess identified above. Model fitting is done via perturbative Hybrid Residual Maximum Likelihood (pHREML; Fleming et al. 2019) estimation, and model selection is based on Akaike's Information Criterion (AIC; Burnham and Anderson 2002, Fleming et al. 2019). For data with evidence of range residency, the set of candidate models includes the IID process, the Ornstein-Uhlenbeck (OU) process (Uhlenbeck and Ornstein 1930), and the

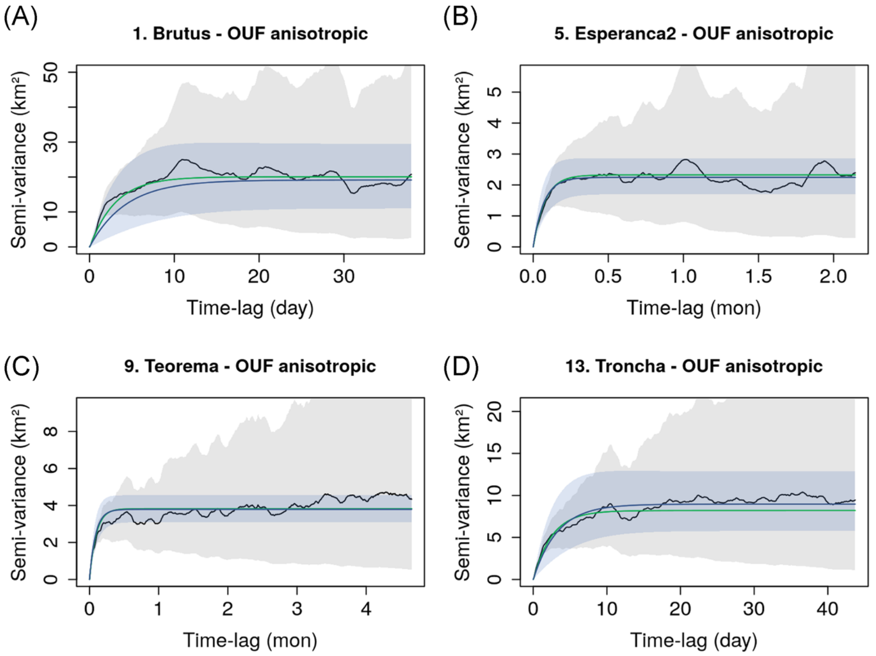


Figure 2. Empirical variograms (black curves and gray confidence envelopes) and semi-variance function of the AIC-best model (blue curves and blue confidence envelopes) for each individual jaguar. The green curves are the semi-variance functions implied by the intial parameter guesses. By default, ctmmweb shows the first 50% of each variogram, in keeping with standard practice in geostatistics. All four jaguars show strong evidence of range residency with each variogram having a clear asymptote, and the OUF-Anisotropic model was selected for all individuals.

OU-Foraging process (OUF; Fleming et al. 2014). The IID process, which is the model assumed by conventional range estimators such as KDE and MCP, has a home range but both positions and velocities are uncorrelated. The OU process features a home range, correlated positions, but uncorrelated velocities (i.e., no directional persistence). Finally, the OUF process is the most general model, and includes a home range, correlated positions, and correlated velocities. Each of these movement processes is considered in both isotropic and anisotropic form. For isotropic models, movement is the same in all directions (i.e., circular home range), while movement may vary by direction for anisotropic models (i.e., non-circular home range). After the fitting and model selection algorithms have run, the selected model is displayed graphically via the variogram for each individual, and the details of the fit are output in a table below the variograms. For each individual, the AIC-best model is highlighted by default in the results table, and will be used as the basis for the conditional analyses that follow. If desired (i.e., for comparative purposes), the user can choose to base downstream conditional analyses on any other model in the results table by manually selecting it. As a rule, however, optimal results will only be obtained by conditioning on the AIC-best model for each individual. The parameter estimates displayed in the table for each model may also be of interest. For example, the parameter τ [position] gives the average time it takes the focal individual to cross the linear extent of its home range. It is important to realize that because ctmmweb is considering many different autocorrelation models in the background (instead of assuming the model *a priori* as in conventional movement analyses), the model selection step is computationally intensive and can take substantial time for large datasets.

Home Range

Autocorrelated kernel density estimation home range analysis can be based on any range-resident movement model supported by ctmmweb. Importantly, AKDE based on the IID model reduces exactly to conventional KDE with the Gaussian reference function bandwidth optimizer (Fleming et al. 2015). In other words, for a dataset with statistically independent locations, ctmmweb will select the IID model as AIC-best, and a conventional KDE estimate will be produced. If instead the data are autocorrelated, the most appropriate autocorrelated movement model (either OU or OUF) will be selected and used as the basis for AKDE. Assuming a one-size-fits-all model *a priori*, like conventional home range estimators do via their IID assumption, can result in home ranges that are underestimated in proportion to the strength of autocorrelation in the data. Autocorrelation driven underestimation of home range areas can be avoided by letting the data inform the choice of an appropriate autocorrelated movement model via model selection. After all, it is not autocorrelation *per se* that causes problems, but rather unmodeled autocorrelation and the resulting violation of the IID assumption made by conventional estimators.

After model fitting and selection has finished, selecting the Home Range page from the navigation panel will automatically calculate and plot AKDE estimates for each individual. The app also provides a table of summary statistics about the AKDE estimates, including the area corresponding to the focal percentile of the range distribution (95% by default, but user adjustable), as well as confidence intervals for each estimate.

Overlap

As individuals, by definition, perform most of their movements within their home ranges, one can expect home range overlap to be proportional to encounter rates among individuals (Martinez-Garcia et al. 2020). Thus, overlap can serve as a useful proxy for interaction potential. After home range estimation, pairwise overlap among individuals can be estimated via the Overlap page. In ctmmweb, overlap is quantified by the widely-used Bhattacharyya coefficient (Fieberg and Kochanny 2005, Winner et al. 2018), which is a symmetric index and ranges between 0 (no overlap) and 1 (complete overlap). When overlap analysis is the goal, AKDE home ranges must be calculated on the same grid, which is the default choice but may come at the expense of longer run times.

Map

To help contextualize the results, ctmmweb allows both the data and home range estimates to be plotted on an interactive map provided by the R interface to the Java Leaflet library (Cheng et al. 2018). The user can select which individuals, and which elements for each individual (data and/or home range estimates), to display. Furthermore, the user can choose among a range of map options including terrain, satellite, and topographic backgrounds.

STUDY AREA

To demonstrate the utility of ctmmweb, we used GPS data from four jaguars (one male and three females) tracked in the Brazilian Pantanal from 2013 to 2015 (Morato et al. 2018). For convenience we will later refer to these individuals by the names they have been given in the dataset. The three females were named Esperanca2, Teorema, and Troncha, while the male was named Brutus. With an estimated area of 150,355 km^2, the Pantanal was the world's largest tropical wetland, and was a biome in which jaguars were considered to be vulnerable (Morato et al. 2016). Jaguars are medium-sized (ca. 75 kg), range-resident carnivores that cross their home ranges on hourly timescales (Morato et al. 2016). For these individuals, locations were collected at hourly intervals for 141 days on average (range = 76–274 days) via Lotek/Iridium GPS collars, resulting in a mean of 2480 recorded locations per animal (range = 1323–4860).

RESULTS

Using the jaguar data, we completed all steps of the workflow from import through conditional analyses including AKDE home range estimation and home range overlap via the Bhattacharyya coefficient. At the end of the analysis session we saved our results using the Save Progress button at the bottom of ctmmweb's side bar (Fig. 1).

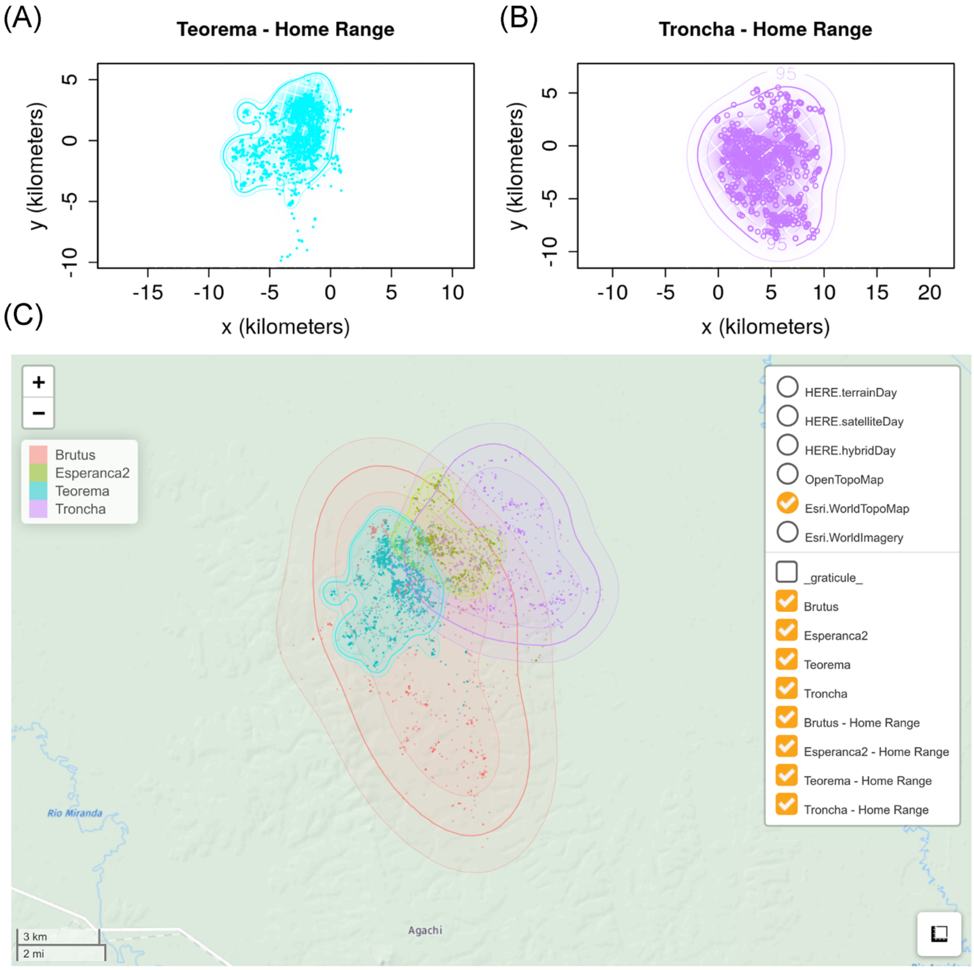
All four jaguars show clear range residency, as evidenced by the pronounced asymptotes in their empirical variograms (Fig. 2). For all four individuals the OUF-Anisotropic model was unequivocally selected, with AIC differences in favor of this model >8 in all cases, and >69 in two out of four cases (see the model selection results table in the work report, available online in Supporting Information Report S1). The model features correlated positions, correlated velocities (directional persistence), and a home range, and all of these features were apparent in the empirical variograms of the jaguars (Fig. 2). The anisotropic moniker on the selected model name implies that each animal's movement was spatially asymmetrical, i.e., greater in some directions than in others.

We next computed AKDE home range estimates for all four individuals, which ctmmweb displays individually on the Home Range page (Fig. 3, top row). Notice the grid superimposed on the background of the density estimates. The size of the grid depicts the bandwidth size and represents the spatial resolution of the home range estimate. Features apparent in the home range (e.g., holes) that are smaller than the grid should be ignored because they are below the spatial resolution of the estimate and thus could be spurious. Said another way, the grid represents the finest spatial scale that can be accurately resolved by the home range estimate. The data and home range estimates from all four animals were also overlaid on a topographical map, using ctmmweb's interactive Map page (Fig. 3). Viewing the home range estimates together suggests significant pairwise overlap among individuals, particularly for the lone male jaguar, Brutus, with the three females.

To properly quantify overlap, we calculated the Bhattacharyya coefficient via ctmmweb's Overlap page, given the AKDE estimates previously calculated (Fig. 4). All pairwise overlaps were statistically significant, with lower confidence limits not including zero overlap (Fig. 4). However, the average overlap of the lone male with the females (0.52 [0.41, 0.63]; point estimate with 95% confidence intervals) was significantly greater ($P < 0.05$) than average pairwise overlap among females (0.33 [0.25, 0.40]). Additionally, the estimated difference between M-F and F-F overlap was 0.20 [0.06, 0.33]. Additional results from the jaguar analysis can be found in the Supporting Information in the online version of this article.

DISCUSSION

Autocorrelation has become a critical issue in animal tracking data that can no longer be ignored. Analyses based on such data will either have to account for autocorrelation or risk being systematically, and often grossly, biased. Fortunately, substantial progress in accounting for autocorrelation in animal tracking analyses has been made in recent years. The bulk of these advances, however, have heretofore only been accessible in command-line analysis packages such as ctmm (Fleming and Calabrese 2015, Calabrese et al. 2016), crawl (Johnson et al. 2008), move (Kranstauber and Smolla 2013), corrMove (Calabrese et al. 2018), and marcher (Gurarie et al. 2017). Of these, ctmm covers a



○ HERE.terrainDay
○ HERE.satelliteDay
○ HERE.hybridDay
○ OpenTopoMap
● Esri.WorldTopoMap
○ Esri.WorldImagery
☐ _graticule_
☑ Brutus
☑ Esperanca2
☑ Teorema
☑ Troncha
☑ Brutus - Home Range
☑ Esperanca2 - Home Range
☑ Teorema - Home Range
☑ Troncha - Home Range

Figure 3. AKDE estimates (density + contours) and data (filled circles) for jaguars A) Teorema and B) Troncha, as they are displayed on the Home Range page of the app. Notice the bandwidth grid in the background of these two estimates. C) AKDE home range estimates, together with the location data, for all four individuals plotted on an interactive topological map via the Map page. All estimates display the 95% contour of the range distribution (thick curve) and the 95% confidence envelopes (thin curves) on the contour estimates.

wider range of models and autocorrelation-explicit analyses, and ctmmweb provides easy point-and-click access to the vast majority of analyses supported by ctmm, including AKDE home range estimation. An additional advantage of ctmmweb, is that all of the statistical estimates it produces are accompanied by confidence intervals. To our knowledge, no other software packages besides ctmmweb and ctmm provide confidence intervals on home range and overlap estimates.

Focusing on data from four jaguars in Brazil, we have demonstrated how ctmmweb can be used to visualize and understand key features in tracking data, fit and select appropriate movement models, and perform conditional analyses such as AKDE home range estimation and home range overlap estimation. Home range estimates were very similar to those previously reported for these four jaguars by Morato et al. (2016), with minor differences accounted for by refinements made to the underlying ctmm package since that previous study. In contrast, the overlap estimates reported here for the jaguars are novel and demonstrate lower pairwise overlap of home ranges among neighboring females than among male-female pairs. These overlap results are consistent with reports from the literature on both territoriality among females, and on male home ranges overlapping with multiple females (Schaller and Crawshaw 1980, Rabinowitz and Nottingham 1986). Furthermore, it is also the spatial arrangement expected under the jaguars' social structure (Lukas and Clutton-Brock 2013).

In addition to the capabilities we demonstrated here, ctmmweb inherits many of the under-the-hood features of ctmm, including computational algorithms that are highly efficient and scale well to large datasets. The app also has considerably more analytical functionality, including: 1) the ability to accommodate information on telemetry error in all analysis steps, including model fitting/selection and subsequent conditional analyses; 2) scale-free estimation of speed and distance traveled using conditional simulation (Noonan et al. 2019); 3) advanced options for detecting and accounting for multiple sampling schedules in a tracking data; 4) visual subsetting of individual datasets; 5) the ability to detect multiple processor cores and appropriately distribute analyses over them to reduce run time; 6) the ability to perform optimally weighted AKDE home range estimation on irregularly sampled data (Fleming et al. 2018);

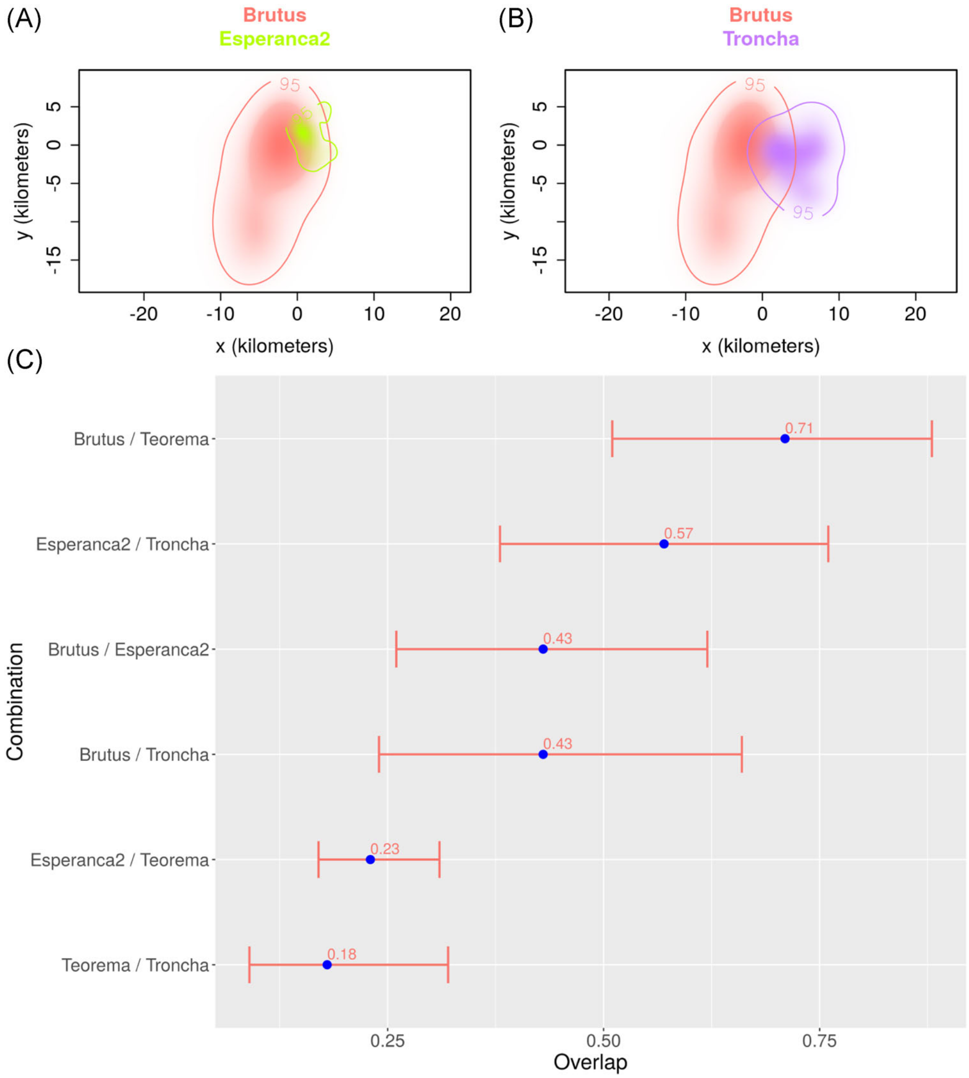


Figure 4. Visual representation of pairwise home range overlap based on the estimated AKDE densities for jaguars A) Brutus/Esperanca2 and B) Brutus/Troncha. C) Pairwise overlap estimates based on the Bhattacharyya coefficient (blue points) and 95% confidence intervals (red bars) for all possible pairs of individuals.

and 7) occurrence distribution estimation via time-series kriging (Fleming et al. 2016).

Ctmmweb is openly available in cloud-hosted form, which requires no installation or configuration, and is also available as a locally installable R package via GitHub (https://github.com/ctmm-initiative/ctmmweb), including a wizard-style installer for Windows operating systems. Links to all versions, as well as to other ctmmweb-related resources can be found in Supporting Information Report S2 in the online version of this article. For first-time users and quick, exploratory analyses, we recommended the cloud-hosted version, while for more thorough analysis or regular use, we recommend installing ctmmweb locally. To help improve the app going forward, bug reports, suggestions for improvement, or other feedback can be posted on GitHub.

We will continue to expand and refine ctmmweb's capabilities as the ctmm package, and the analytical platform it is based on, continue to develop. Currently, ctmmweb is the only point-and-click platform that supports AKDE home range estimation, and it also facilitates many other autocorrelation-explicit analyses. We intend ctmmweb to make these sophisticated movement tools accessible to a broader range of ecologists, wildlife professionals, and conservation biologists, without requiring advanced knowledge of R programming.

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Additional supporting information may be found in the online version of this article at the publisher's website. Supporting Information S1 includes the full session archive from the jaguar analysis session, and a separate description of the contents of the session archive. Supporting Information S2 includes links to online resources for ctmmweb.