Supplementary file 2: Autocorrelation-informed home range estimation with the ctmm R package

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Introduction

Home range estimation is a key output from animal tracking datasets, but the inherent properties of animal movement can lead traditional methods to under- or overestimated their size. **Autocorrelated Kernel Density Estimation (AKDE)** methods were designed to be statistically efficient while explicitly dealing with the complexities and biases of modern movement data, such as *autocorrelation*, *small sample sizes*, and *missing or irregularly sampled data.*

This tutorial is a companion piece to our manuscript *"Autocorrelation-informed home range estimation: a review and practical guide"*. The **AKDE** family of home range estimators will be run using **R software** (https://www.r-project.org/) and the `ctmm` package (Calabrese et al., 2016). For any definitions, check the main manuscript or the *Glossary.* The techniques and mitigation measures available in this package include:

Method	When to run?	What does it do?	R function
AKDE	Tracking data is autocorrelated	Estimates range distributions from autocorrelated data, by conditioning on an autocorrelation model.	`akde(…, debias = FALSE)`
AKDEc	If using GRF-based KDEs (such as AKDE)	Removes the tendency of Gaussian reference function (GRF) methods to overestimate the area of home ranges.	`akde(…, debias = TRUE)`
pHREML	Small (absolute and effective) sample sizes	Improves upon ML and REML autocorrelation estimation, mitigating small sample size biases.	`ctmm.select(…, method = "pHREML")`
wAKDEc	Irregular sampling schedules or missing data	Upweights observations that occur during under-sampled times, while downweighting those occurring during over-sampled times.	`akde(…, weights = TRUE)`
Parametric bootstrap	Extremely small effective sample size	Calculates and corrects for autocorrelation estimation biases, by simulating from an approximate sampling distribution.	`ctmm.boot(...)`

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AKDE$_c$ and pHREML are default arguments within the `akde()` and `ctmm.select()` functions, respectively. Both measures will run automatically if arguments `debias` and `method` are left unspecified. For most situations, we recommend keeping both of these arguments as the default.

```r
# Installing & loading package:
install.packages("ctmm")
library(ctmm)
```

We provide a guide to **home range estimation** using the following workflow:

- **Step 1.** – Formatting and loading an animal tracking dataset;
- **Step 2.** – Checking for the *range residency* assumption;
- **Step 3.** – Selecting the best-fit movement model through *model selection*;
- **Step 4.** – Feeding a movement model into the *home range estimator*;
- **Step 5.** – Evaluating additional *biases*, applying *mitigation measures.*

Data Preparation

We will use two datasets, both available within the `ctmm` package: African buffalos (*Syncerus caffer*), and Mongolian gazelles (*Procapra gutturosa*). Information on the data collection protocol is available in Cross *et al.* (2009) and Fleming *et al.* (2014). The `ctmm` package requires data to conform to Movebank naming conventions (https://www.movebank.org/node/2381). We recommend uploading your data to Movebank (http://www.movebank.org/) as this will facilitate data preparation, and ensure that your data are correctly formatted for `ctmm`. If needed, Movebank allows you to keep your data private.

We will focus on the simplest data structure:

- `animal ID` or `ID` — An individual identifier for each animal tracked;
- `timestamp` or `t` — The date and time corresponding to a sensor measurement;
  - **Example**: 2021-01-01 18:31:00.000
    - **Format**: yyyy-MM-dd HH:mm:ss.SSS
- `longitude` or `x` — The geographic longitude of the location as estimated by the sensor.
  - **Example**: -121.1761111
    - **Units**: decimal degrees, WGS84 reference system.
- `latitude` or `y` — The geographic latitude of the location as estimated by the sensor;

- **Example**: -41.0982423
    * **Units**: decimal degrees, WGS84 reference system.

Location can also be described as UTM locations instead of latitude/longitude. In this case, you should provide `UTM easting`, `UTM northing`, and `UTM zone`. For all terms and conventions, please see the full vocabulary list here: http://vocab.nerc.ac.uk/collection/MVB/current/.

Step 1. – Formatting and loading an animal tracking dataset

You can import data into R through the `read.table()` or `read.csv()` functions; make sure to navigate to the appropriate folder or working directory. For example:

```
# First, list all files in your current directory:
list.files() # make sure this leads to the location of your file
```

```
# Second, load the correct file:
animal0_longlat <- read.csv(here("example_data_longlat.csv"))
head(animal0_longlat)
```

```
##        ID        timestamp longitude latitude
## 1 animal0 2005-07-14 05:35  30.59648 65.24774
## 2 animal0 2005-07-14 07:35  30.53256 65.27085
## 3 animal0 2005-07-14 08:34  30.52398 65.26446
## 4 animal0 2005-07-14 09:35  30.52848 65.25948
## 5 animal0 2005-07-14 10:35  30.53382 65.26643
## 6 animal0 2005-07-14 11:34  30.49970 65.27868
```

```
animal0_utm <- read.csv(here("example_data_utm.csv"))
head(animal0_utm)
```

```
##        ID        timestamp UTM.Easting UTM.Northing UTM.zone
## 1 animal0 2005-07-14 05:35    387730.0      7238204      36N
## 2 animal0 2005-07-14 07:35    384846.3      7240894      36N
## 3 animal0 2005-07-14 08:34    384418.1      7240197      36N
## 4 animal0 2005-07-14 09:35    384606.5      7239634      36N
## 5 animal0 2005-07-14 10:35    384885.8      7240399      36N
## 6 animal0 2005-07-14 11:34    383347.9      7241826      36N
```

```
# Finally, convert to telemetry object:
animal0a <- as.telemetry(animal0_longlat)
```

```
## Minimum sampling interval of 59 minutes in animal0
```

```
animal0b <- as.telemetry(animal0_utm)
```

```
## Geocentric coordinates not found. Looking for UTM coordinates.
## Minimum sampling interval of 59 minutes in animal0
```

```
# if left unspecified, as.telemetry() will assume timezone = UTC
```

Both these files represent the same individual, with either *longitude/latitude*, or UTM coordinates (*easting*, *northing*, and *UTM zone*). The `as.telemetry()` function will immediately identify the columns if they are correctly named, then output the minimum sampling interval for each individual in the dataset. In this example, `animal0` has a minimum sampling interval of 59 minutes.

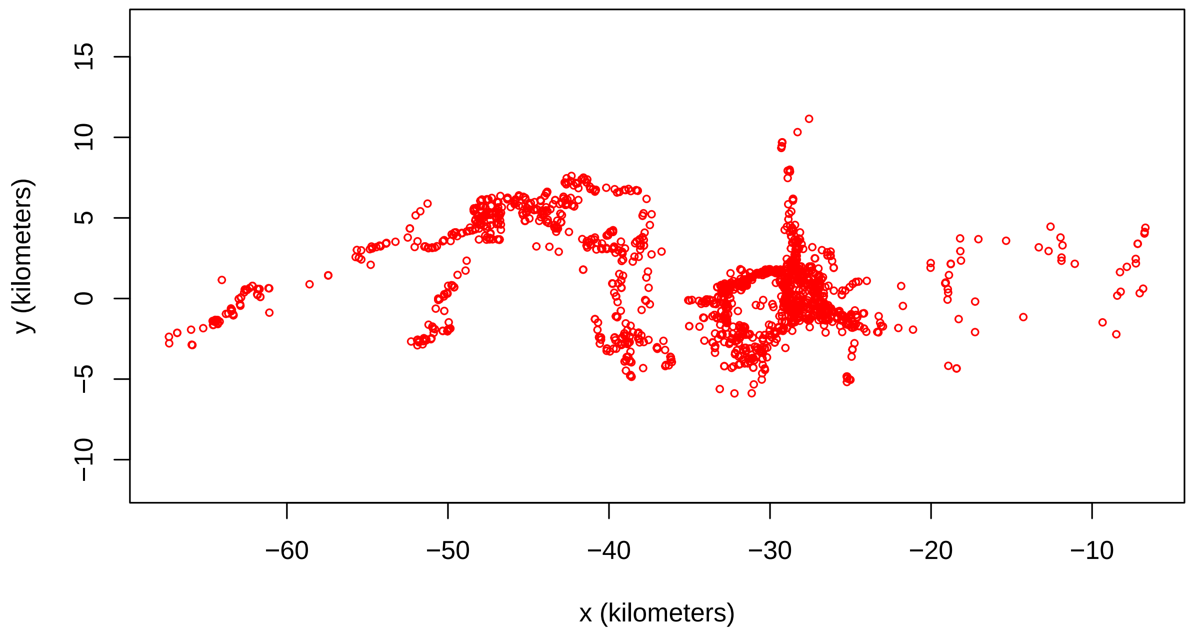
1.1. Buffalo tracking data

For this tutorial, we will use data already prepared into a list of `telemetry` objects. We can load it directly from the `ctmm` R package with the `data()` function:

```
data("buffalo")
animal1_buffalo <- buffalo[[4]] # selecting individual number 4
head(animal1_buffalo)
```

```
##                 timestamp longitude  latitude          t         x         y
## 17517 2006-04-25 05:09:00  31.73749 -24.19705 1145941740 -51803.35 -2715.663
## 17518 2006-04-25 06:09:00  31.73653 -24.19929 1145945340 -51569.29 -2845.660
## 17519 2006-04-25 07:09:00  31.73946 -24.20100 1145948940 -51340.72 -2576.353
## 17520 2006-04-25 08:09:00  31.73987 -24.20092 1145952540 -51344.11 -2533.788
## 17521 2006-04-25 10:09:00  31.74086 -24.20365 1145959740 -51029.45 -2474.771
## 17522 2006-04-25 11:09:00  31.74098 -24.20370 1145963340 -51022.23 -2463.655
```

```
# Plotting locations:
plot(animal1_buffalo)
```



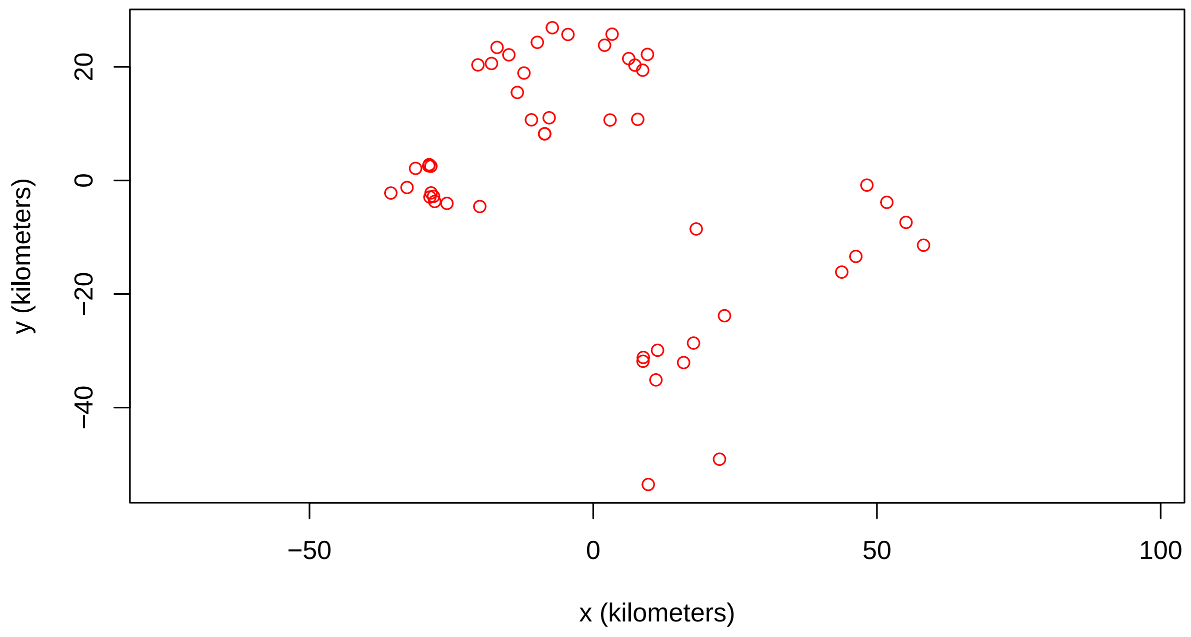
This dataset showcases an irregular sampling schedule: the buffalo nicknamed *"Pepper"* had a sampling rate shift from one fix every hour to one fix every two hours. We will use this dataset to highlight data irregularity and the **wAKDE** mitigation measure.

1.2. Gazelle tracking data

```
data("gazelle")
animal2_gazelle <- gazelle[[11]] # selecting individual number 11
head(animal2_gazelle)
```

```
##               x          y       t
## 2742  18152.70  -8539.799       0
## 2743  15931.16 -32069.788 1306800
## 2744  17678.84 -28632.329 1396800
## 2745  23135.50 -23820.789 1486800
## 2746 -20310.78  20348.792 2419200
## 2747 -17920.31  20598.668 2509200
```

```
# Plotting locations:
plot(animal2_gazelle)
```



Mongolian gazelles have a **home range crossing time** of a few months, and with a maximum longevity around 10 years, it is impossible to get a considerable **effective sample size** no matter the study duration (Fleming et al., 2019). We will use this dataset to highlight how to check **effective sample size** and apply the **parametric bootstrap** mitigation.

Data Analysis

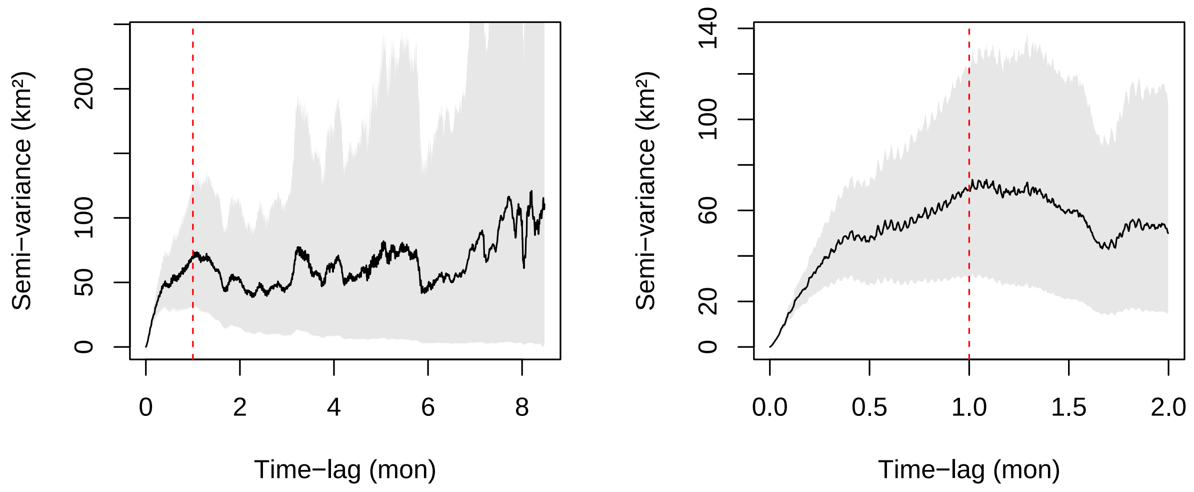
Step 2. – Checking for the *range residency* assumption

First, we want to check if our first tracking dataset (`animal1_buffalo`) can be used for home range estimation by checking for **range residency**. To achieve this, we calculate the **semi-variance function (SVF)**, and visualize it through the `variogram()` function.

Variograms are an unbiased way to visualize *autocorrelation* structure, representing the average square displacement (y-axis) over a specific time lag (x-axis). To facilitate interpretation, we have the **SVF** of `animal1_buffalo` zoomed out (right) to showcase all time lags and (left) zoomed in to showcase time lags up to two months:

```
level <- 0.95 # we want to display 95% confidence intervals
xlim <- c(0,2 %#% "month") # to create a window of 2 months

SVF <- variogram(animal1_buffalo)
par(mfrow = c(1,2))
plot(SVF, fraction = 1, level = level)
abline(v = 1, col = "red", lty = 2) # adding a line at 1 month
plot(SVF, xlim = xlim, level = level)
abline(v = 1, col = "red", lty = 2)
```



We can see that the variogram flattens (*i.e.*, reaches an asymptote) after approximately **1 month** (red line). This also indicates at how coarse the timeseries needs to be to assume independence (no autocorrelation), and corresponds to when traditional methods —such as **minimum convex polygons (MCPs)** and **Kernel Density Estimators (KDEs)**— could be applied without violating their assumptions.

Step 3. – Selecting the best-fit movement model through *model selection*

It is necessary to choose a home range estimator that accounts for the autocorrelated structure of the data, now that we see that it is **not** independently and identically distributed (non-IID). We need to test what movement model may explain the autocorrelated structure of our tracking data. We can run different movement processes with **maximum likelihood (ML)** or other parameter estimators, such as **perturbative Hybrid REML (pHREML)**. To facilitate further comparisons, we will run both ML and pHREML with the `ctmm.select` function.

```
# Calculate an automated model guesstimate:
GUESS1 <- ctmm.guess(animal1_buffalo, interactive = FALSE)
```

```r
# Automated model selection, starting from GUESS:
FIT1_ML <- ctmm.select(animal1_buffalo, GUESS1, method = 'ML')
FIT1_pHREML <- ctmm.select(animal1_buffalo, GUESS1, method = 'pHREML')
## reminder: it will default to pHREML if no method is specified.
```

```r
summary(FIT1_ML)
```

```
## $name
## [1] "OUF anisotropic"
##
## $DOF
##      mean      area     speed
##  11.24296  20.01326 747.72143
##
## $CI
##                                 low       est       high
## area (square kilometers) 431.446013 706.20245 1047.55828
## t[position] (days)         6.775273  12.18604   21.91786
## t[velocity] (minutes)     31.861346  35.81413   40.25730
## speed (kilometers/day)    15.948352  16.54124   17.13385
```

```r
summary(FIT1_pHREML)
```

```
## $name
## [1] "OUF anisotropic"
##
## $DOF
##      mean      area     speed
##  10.34454  15.65772 746.09401
##
## $CI
##                                 low       est       high
## area (square kilometers) 439.064822 773.50766 1201.09155
## t[position] (days)         6.664052  13.36206   26.79221
## t[velocity] (minutes)     31.807736  35.75689   40.19636
## speed (kilometers/day)    15.949646  16.54326   17.13658
```

Within these summaries, `$name` provides the selected best-fit model, `$DOF` provides information on the degrees of freedom (where `$DOF["area"]` corresponds to the **effective sample size** of the home-range area estimate), and `$CI` are the parameter outputs (area, position autocorrelation timescale, velocity autocorrelation timescale, and speed).

The typical pool of candidate models includes isotropic (when diffusion is the same in every direction; symmetrical) and anisotropic (when diffusion varies with direction; asymmetrical) variants. The automated model selection shows that *OUF anisotropic* (anisotropic Ornstein-Uhlenbeck foraging process) is our best-fit model. This movement process features a home range, correlated positions, and correlated velocities. To check the full model selection table, we can run the following command:

```
FIT1_pHREML_verbose <- ctmm.select(animal1_buffalo, GUESS1, verbose = TRUE)
summary(FIT1_pHREML_verbose)
```

	ΔAICc	ΔRMSPE (km)	DOF[area]
OUF anisotropic	0.0000	2.224045	15.657669
OU anisotropic	295.0898	2.634793	9.638283
OUF isotropic	330.2236	3.564231	11.204035
OUf anisotropic	1890.8878	0.000000	333.620712

By adding the argument `verbose = TRUE` we have access to the model selection table. By default, model selection is based on *Akaike's Information Criterion adjusted for small sample sizes* (AICc). The `ctmm` package also offers BIC, LOOCV, and HSCV. LOOCV seems to work slightly better for very small datasets, but we recommend AICc for the majority of datasets.

Step 4. – Feeding a movement model into the *home range estimator*

Now we can fit this movement process into the `akde()` function, and estimate the home range of `animal1_buffalo`. This function currently defaults to the **area-corrected AKDE**, or **AKDEc** (Fleming & Calabrese 2017):

```
# Run an area-corrected AKDE:
UD1_ML <- akde(animal1_buffalo, FIT1_ML)
UD1_pHREML <- akde(animal1_buffalo, FIT1_pHREML)
```

```
summary(UD1_pHREML)$CI # home range area estimation
```

```
##                                   low      est     high
## area (square kilometers) 429.6573 756.9343 1175.357
```

We have calculated our home range for `animal1_buffalo`, resulting in an estimation of 757 km^2 (with 95% confidence intervals: 430–1,175 km^2).

Step 5. – Evaluating additional *biases*, applying *mitigation measures*

5.1. Buffalo tracking data

```
summary(UD1_pHREML)$DOF["area"] # effective sample size of animal1
```

```
##     area
## 15.65772
```

```
nrow(animal1_buffalo) # absolute sample size
```

```
## [1] 1725
```

Our output here also reveals more information regarding our dataset: the **effective sample size (N)** and the **absolute sample size (n)**. We can return this measure with the `summary` function: in our case, the N for `animal1_buffalo` is 15.7. Comparatively, our **absolute sample size** is easy to output, as it is the total number of observations within our dataset (n = 1,725).

As mentioned earlier, `animal1_buffalo` had a device malfunction that led GPS fixes to shift from one fix per hour, to one fix every two hours. As such, this individual is particularly suited for a **weighted AKDEc** (or **wAKDEc**), so we can re-run the function with weights set to `TRUE`:

```
UD1w_pHREML <- akde(animal1_buffalo, FIT1_pHREML, weights = TRUE)
```

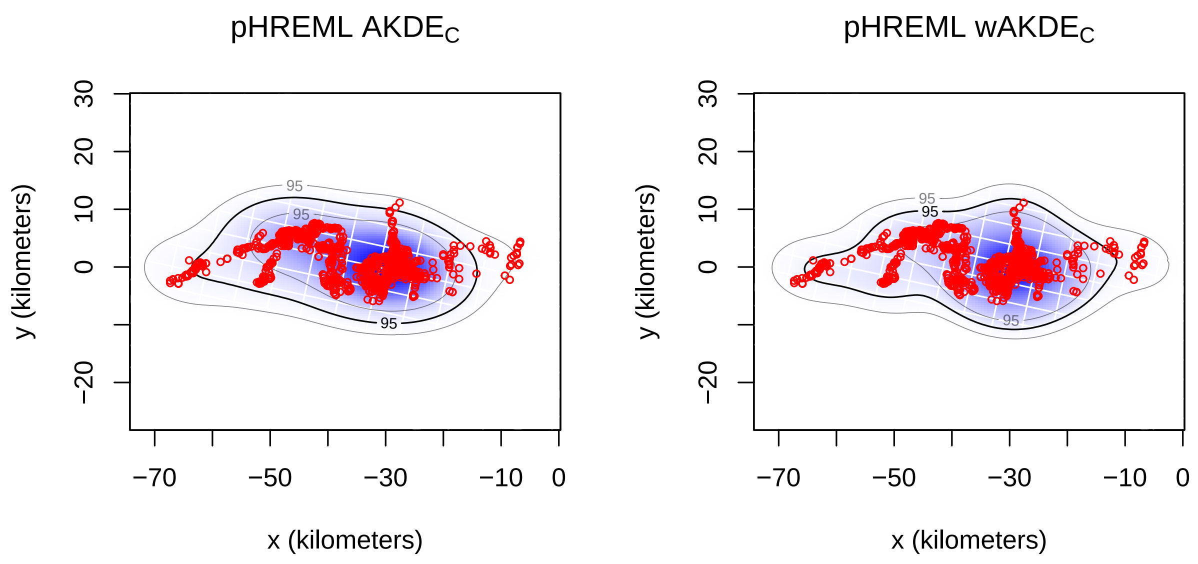
```
summary(UD1w_pHREML)$CI # home range area estimation (weighted)
```

```
##                                 low      est     high
## area (square kilometers) 432.2234 761.4551 1182.376
```

Our new home range area estimation for `animal1_buffalo` is 761 km^2 (with 95% confidence intervals: 432–1,182 km^2). We can now plot our home range estimate for `animal1_buffalo`:

```
# Creating an extent that includes both UDs at the 95% CI level:
EXT <- extent(list(UD1_ML, UD1_pHREML, UD1w_pHREML), level = 0.95)

# Plotting pHREML (with and without weights) side-by-side:
par(mfrow = c(1,2))
plot(animal1_buffalo, UD = UD1_pHREML, ext = EXT)
title(expression("pHREML AKDE"["C"]))
plot(animal1_buffalo, UD = UD1w_pHREML, ext = EXT)
title(expression("pHREML wAKDE"["C"]))
```



For `animal1_buffalo`, the difference between model parameter estimators is not substantial; we only have a ~5.7% AKDE area underestimation by ML compared to pHREML. However, the data fits the spatial locations much better.

```
( 1 - summary(UD1_ML)$CI[1,2] / summary(UD1w_pHREML)$CI[1,2] ) * 100
```

```
## [1] 5.742588
```

5.2. Gazelle tracking data

We can also check the difference with `animal2_gazelle`'s tracking data, where the small **effective sample size** issue is clearer:

```
GUESS2 <- ctmm.guess(animal2_gazelle, interactive = FALSE)

FIT2_ML <- ctmm.select(animal2_gazelle, GUESS2, method = 'ML')
FIT2_pHREML <- ctmm.select(animal2_gazelle, GUESS2, method = 'pHREML')

UD2_ML <- akde(animal2_gazelle, FIT2_ML)
UD2_pHREML <- akde(animal2_gazelle, FIT2_pHREML)
```

With `animal2_gazelle`, we have a more substantial area underestimation by ML compared to pHREML (~15.2%). We can also see that our *effective sample size* is only 4.5, with an *absolute sample size* of 49 ($N \ll n$).

```
( 1 - summary(UD2_ML)$CI[1,2] / summary(UD2_pHREML)$CI[1,2] ) * 100
```

```
## [1] 15.19245
```

```
summary(UD2_pHREML)$DOF["area"] # effective sample size
```

```
##     area
## 4.528926
```

```
nrow(animal2_gazelle) # absolute sample size
```

```
## [1] 49
```

At this point, we have selected a movement process, fed it into a home range area estimation with different model parameter estimators, and corrected for irregular sampling rates. With **small effective sample sizes**, it is important to see if **parametric bootstrapping** may be worth it to further reduce our estimation error. In order to do so, we can check the expected order of bias from pHREML:

```
# Expected order of pHREML bias:
1/summary(FIT2_pHREML)$DOF['area']^2
```

```
##       area
## 0.04875392
```

The bias is currently $\mathcal{O}(5\%)$ ("in the order of" 5%). As such, we will run parametric bootstrapping for `animal2_gazelle`. The relative error target is 1% by default (`argument error = 0.01`), but can be adjusted if necessary.

```
start_time <- Sys.time() # start recording running time
BOOT <- ctmm.boot(animal2_gazelle, FIT2_pHREML, trace = 2)
## note: this function incurs substantial computational cost, may take hours.
( total_time <- Sys.time() - start_time ) # output running time
```

```
summary(BOOT)
```

```
## $name
## [1] "OUF isotropic"
##
## $DOF
##      mean      area     speed
##  3.196957  3.530735 10.000358
##
## $CI
##                                low          est         high
## area (square kilometers) 3429.704883 14089.021613 32137.455223
## t[position] (months)        0.000000     1.781242     3.758819
## t[velocity] (hours)         2.248230    10.481973    48.870349
## speed (kilometers/day)      5.590052     8.072361    10.551247
```

```
1/summary(BOOT)$DOF['area']^3 # expected order of bias
```

```
##       area
## 0.02271981
```

We can see that the expected order of bias was reduced to 2.3%, which is comparable to the numerical error target of 1%. To reduce the numerical error further, we would need to change the default relative error target of `ctmm.boot`, but the computational cost would continue to increase, and the comparably large statistical bias (2%) would remain.

Now we will calculate the **AKDEc** based on the estimated parameters, and plot the home range of `animal2_gazelle`. Because of small **effective sample size**, we set optimal weights to `TRUE` for improved statistical efficiency:

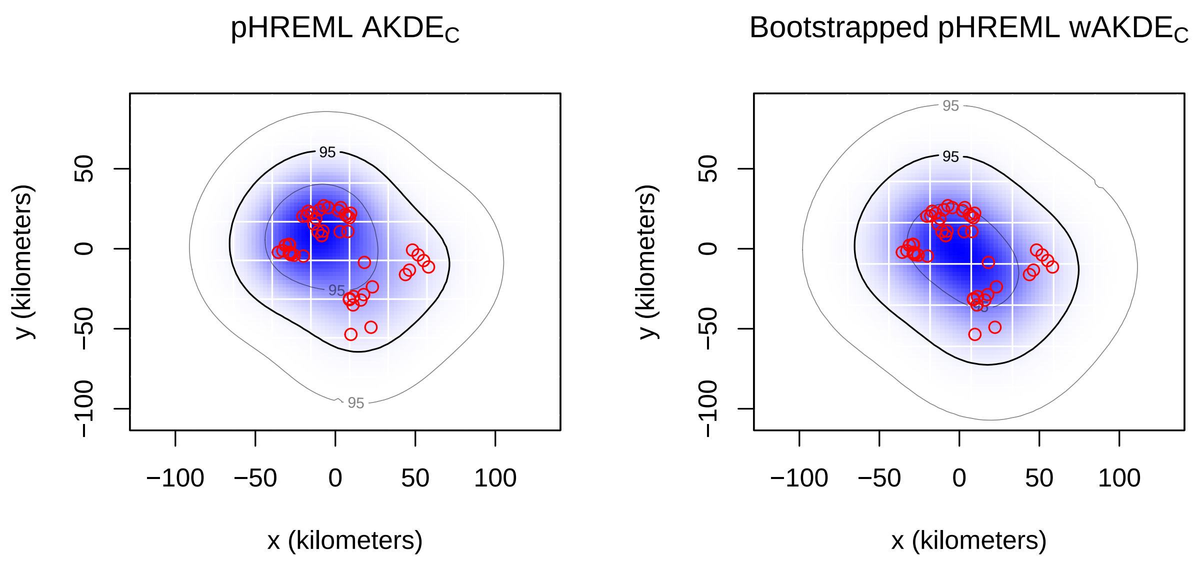
```
UD2_bpHREML <- akde(animal2_gazelle, BOOT, weights = TRUE)
summary(UD2_bpHREML)$CI
```

```
##                               low      est     high
## area (square kilometers) 3231.504 13274.82 30280.25
```

Finally, we have calculated our home range for `animal2_gazelle`, with an estimated area of 13,274 square kilometers (with 95% confidence intervals: 3,231–30,280 km^2). Our uncertainty with `animal2_gazelle` is substantially higher than with `animal1_buffalo`, as expected due to the small **effective sample size**.

```r
# Creating an extent that includes both UDs at the 95% CI level:
EXT <- extent(list(UD2_pHREML, UD2_bpHREML), level = 0.95)

# Plotting pHREML and bootstrapped-pHREML side-by-side:
par(mfrow = c(1,2))
plot(animal2_gazelle, UD = UD2_pHREML, ext = EXT)
title(expression("pHREML AKDE"["C"]))
plot(animal2_gazelle, UD = UD2_bpHREML, ext = EXT)
title(expression("Bootstrapped pHREML wAKDE"["C"]))
```



The results presented here were generated with `R` version `4.1.1`, and `ctmm` version `0.6.0`.

Glossary

– *Home range*: the area repeatedly used throughout an animal's lifetime for all its normal behaviors and activities, excluding occasional exploratory moves.

– *Range residency*: the tendency of an animal to remain within their home range.

– *Home range crossing time*: the time required for an animal to cross the linear extent of its home range.

– *Absolute sample size* (n): the observations in a dataset.

– *Effective sample size* (N): number of range crossings that occurred during the observation period. Can be roughly estimated by dividing the duration of the tracking dataset by the average *home range crossing time* parameter.

References

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