Guide to autocorrelated home range estimation

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This tutorial is a companion piece to our manuscript ***"Autocorrelation-informed home range estimation: a review and practical guide"***. Manuscript was published in Methods in Ecology and Evolution. Preprint is also available on EcoEvoRxiv. For any definitions, check the main manuscript or the *Glossary*.

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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*.

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). The techniques and mitigation measures available within this package include:

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

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(...)`

unspecified. For most situations, we recommend keeping both of these arguments as the default.

```
# 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. You can find two example files within the GitHub repository data folder. To read these .csv files into R:

```
install.packages("here")
library(here)

here() # your working directory

# First, list all files in a specific folder:
list.files("data") # verify that your file appears here
```

```
# Then load the file:
animal0_longlat <- read.csv(here("data/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
```

```
# or:
animal0_utm <- read.csv(here("data/example_data_utm.csv"))
head(animal0_utm)
```

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

```
# Finally, convert to telemetry object:
animal0a <- as.telemetry(animal0_longlat)
animal0b <- as.telemetry(animal0_utm)
# if left unspecified, as.telemetry() will assume timezone = UTC, datum = WGS84
```

Both these files represent the same individual, with either *longitude*/*latitude*, or UTM coordinates (*easting*, *northing*, and *zone*), and both outputs —`animal0a` and `animal0b`— will show the same coordinates after conversion. In general, the `as.telemetry()` function will immediately identify the columns if they are correctly named, convert the projection if needed, and 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

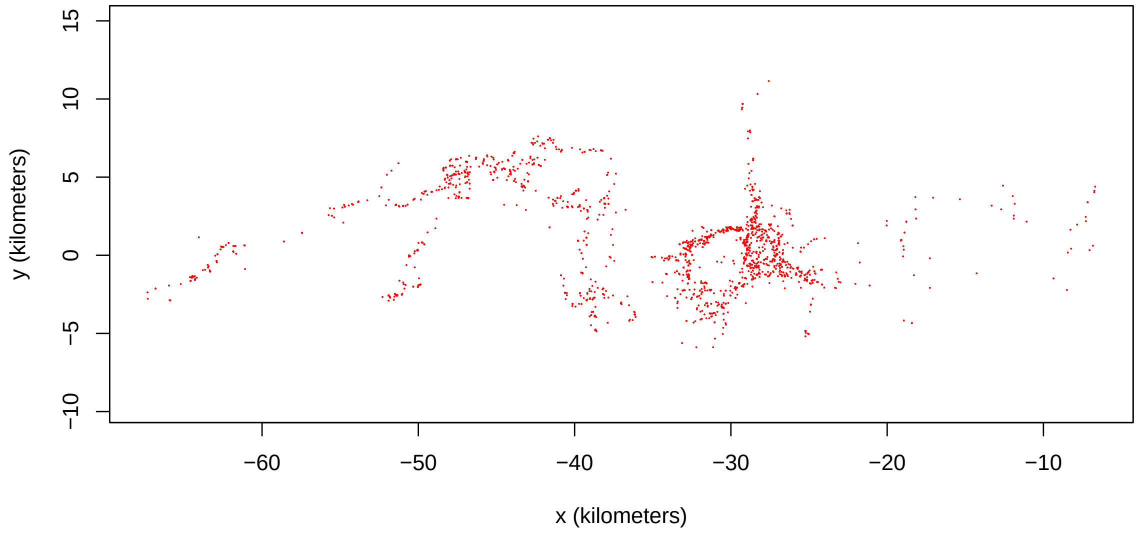
For this tutorial, we will use data already prepared into a list of `telemetry` objects. We can load it directly from the `ctmm` R package with the `data()` function:

```
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.

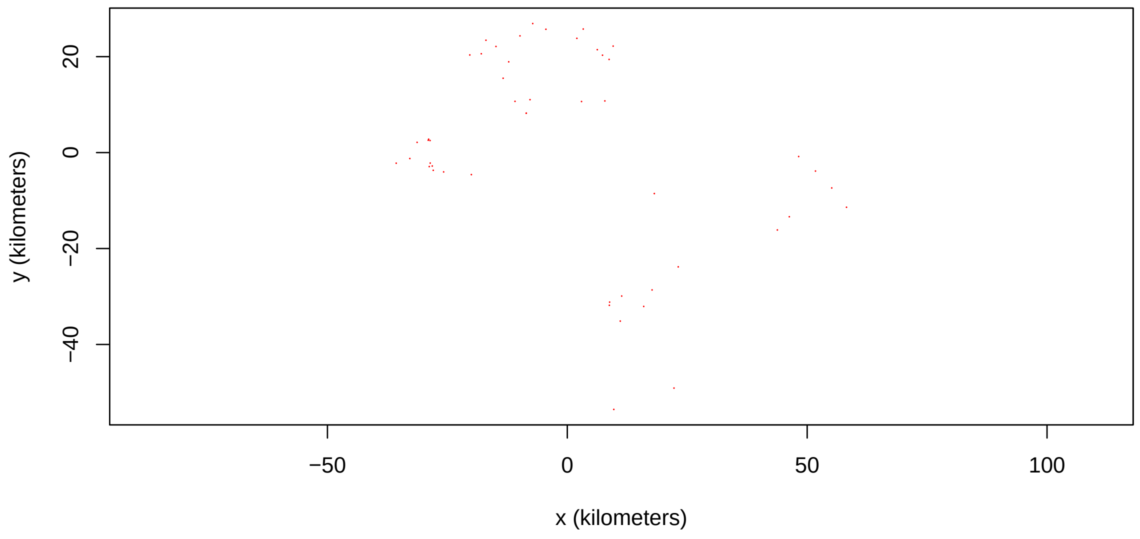
1.2. Gazelle tracking data

```
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

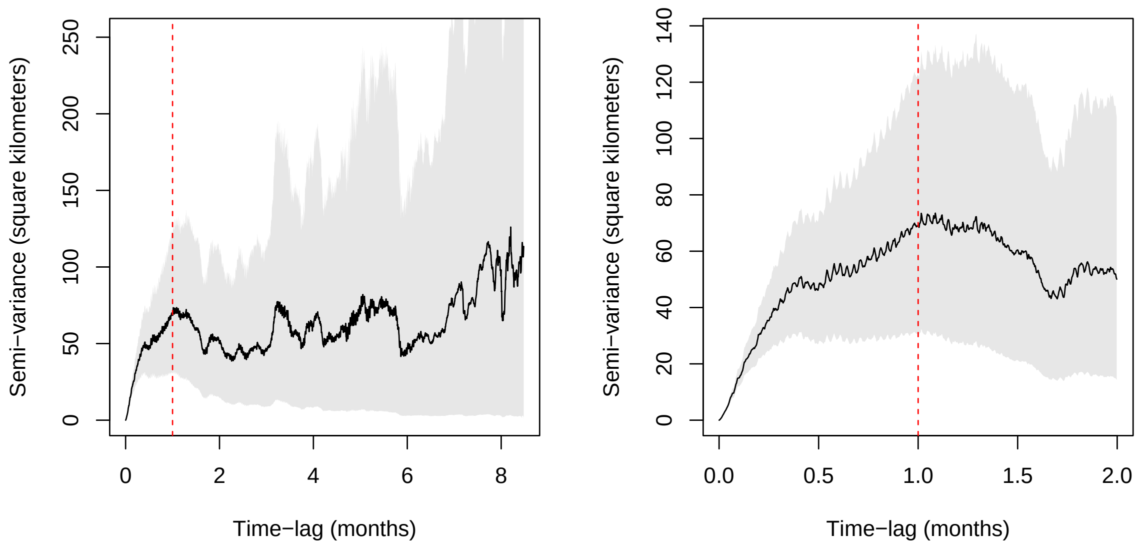
Step 2. – Checking for the *range residency* assumption

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)

# 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.

summary(FIT1_ML)
summary(FIT1_pHREML)
```

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)
```

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):

::: {.cell}

```
# 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
```

:::

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
15.65773
```

```
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).

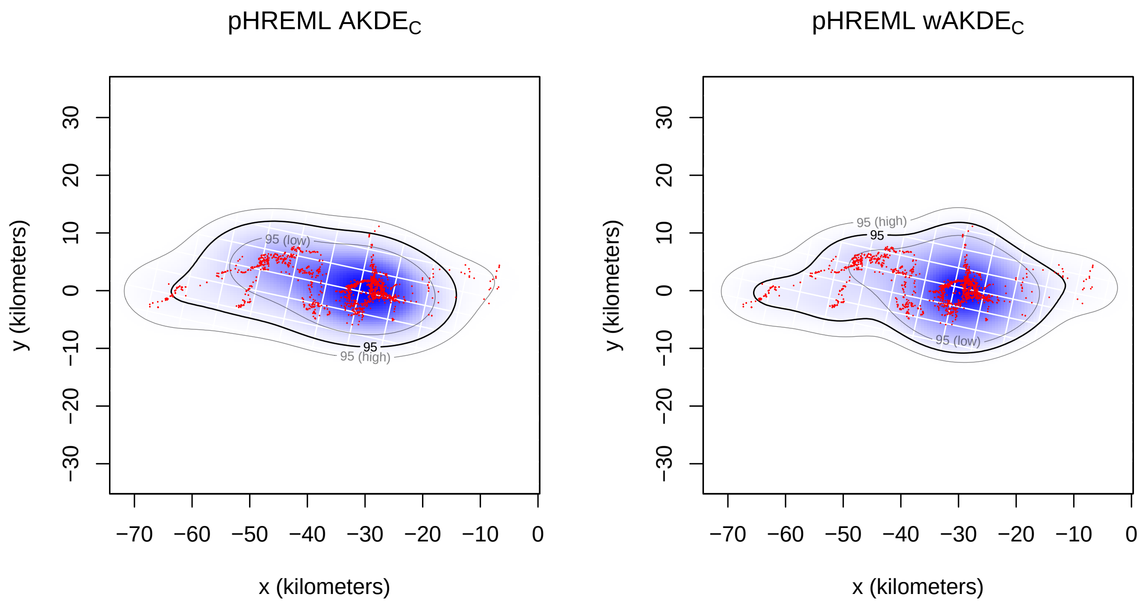
As mentioned earlier, `animal1_buffalo` had a device malfunction that led GPS fixes to shift from one fix per hour, to one fix every two hours. As such, this individual is particularly suited for a **weighted AKDEc** (or **wAKDEc**), so we can re-run the function with weights set to `TRUE`:

```r
UD1w_pHREML <- akde(animal1_buffalo, FIT1_pHREML, weights = TRUE)
summary(UD1w_pHREML)$CI # home range area estimation (weighted)
```

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`:

```r
# 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] 5.737587
```

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] 15.16696
```

```
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
0.04875393
```

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
```

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

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.

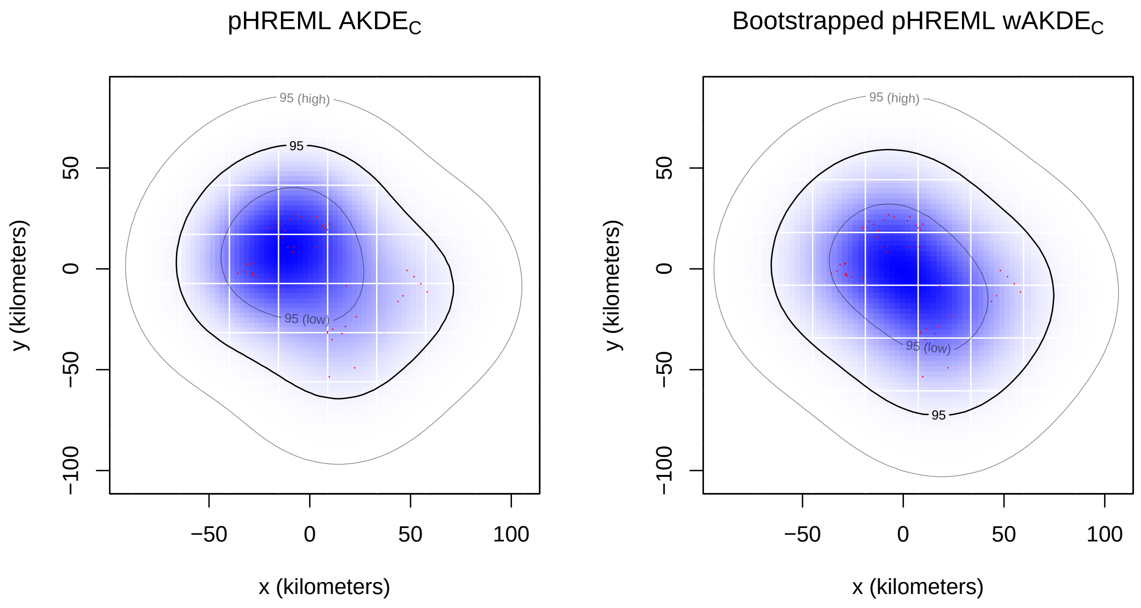
Now we will calculate the **AKDEc** based on the estimated parameters, and plot the home range of `animal2_gazelle`. Because of small ***effective sample size***, we set optimal weights to `TRUE` for improved statistical efficiency:

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

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 `4.2.3`, and `ctmm` version `1.1.1`.

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 number of observations (fixes) 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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