ANIMOVE 2022

CONTINUOUS-TIME MOVEMENT MODELS

Center for Advanced Systems Understanding (CASUS)
Helmholtz-Zentrum Dresden-Rossendorf (*HZDR*)

HOME RANGE ESTIMATION

USING THE CTMM R PACKAGE

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THEORY

PRACTICE

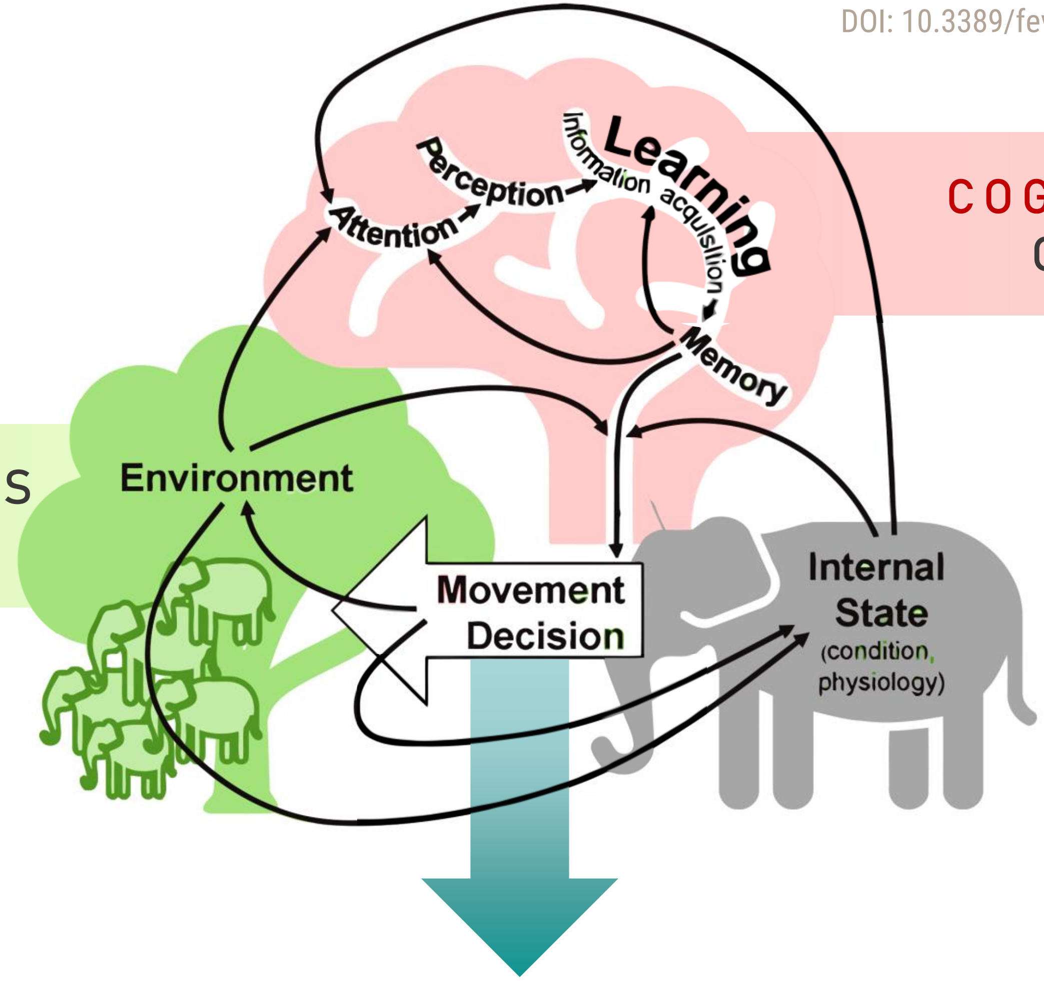
ANIMAL MOVEMENT

Modified from Lewis *et al.* (2021)
DOI: 10.3389/fevo.2021.681704

We cannot separate movement from space-use.

COGNITIVE DRIVERS OF MOVEMENT

ENVIRONMENTAL DRIVERS OF MOVEMENT



MOVEMENT TRAJECTORIES

Animal movement is autocorrelated.

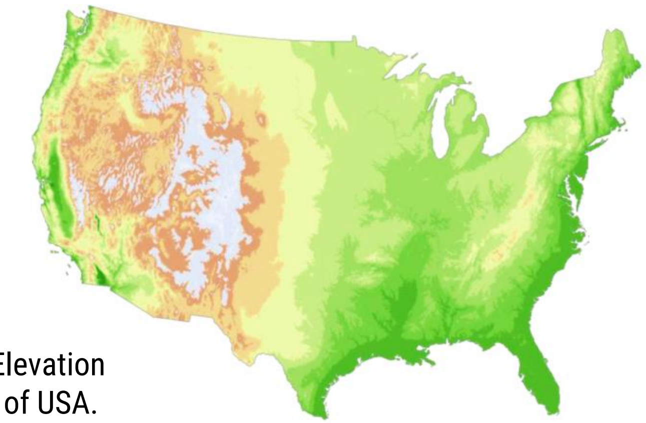
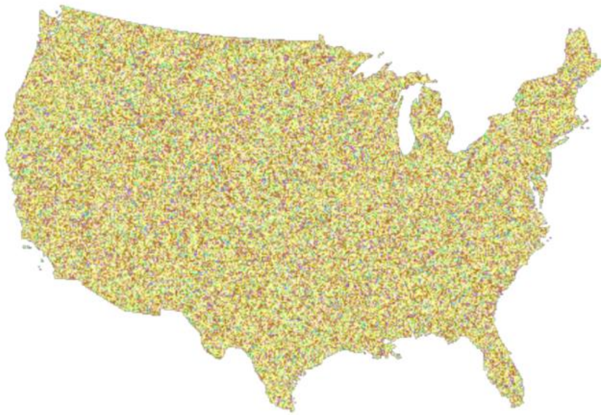


Fig. Elevation map of USA.

If features were not autocorrelated



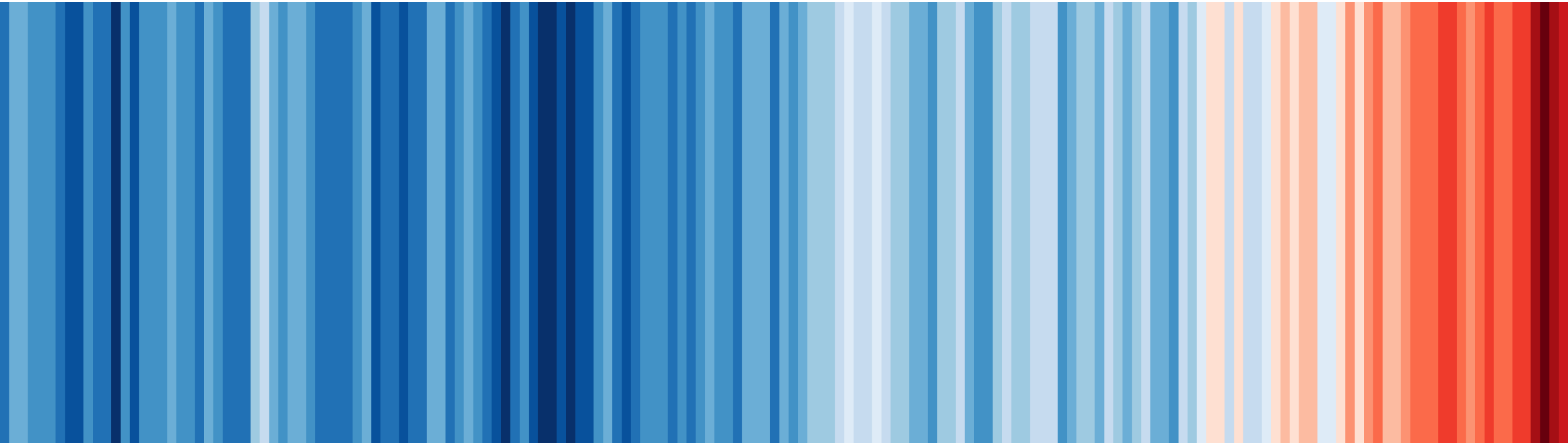
First Law of Geography

"Everything is related to everything else, but near things are more related than distant things".

Tobler (1970)

If not accounted for, non-independence can seriously undermine inferences and lead to overconfidence.

Autocorrelation is informative.



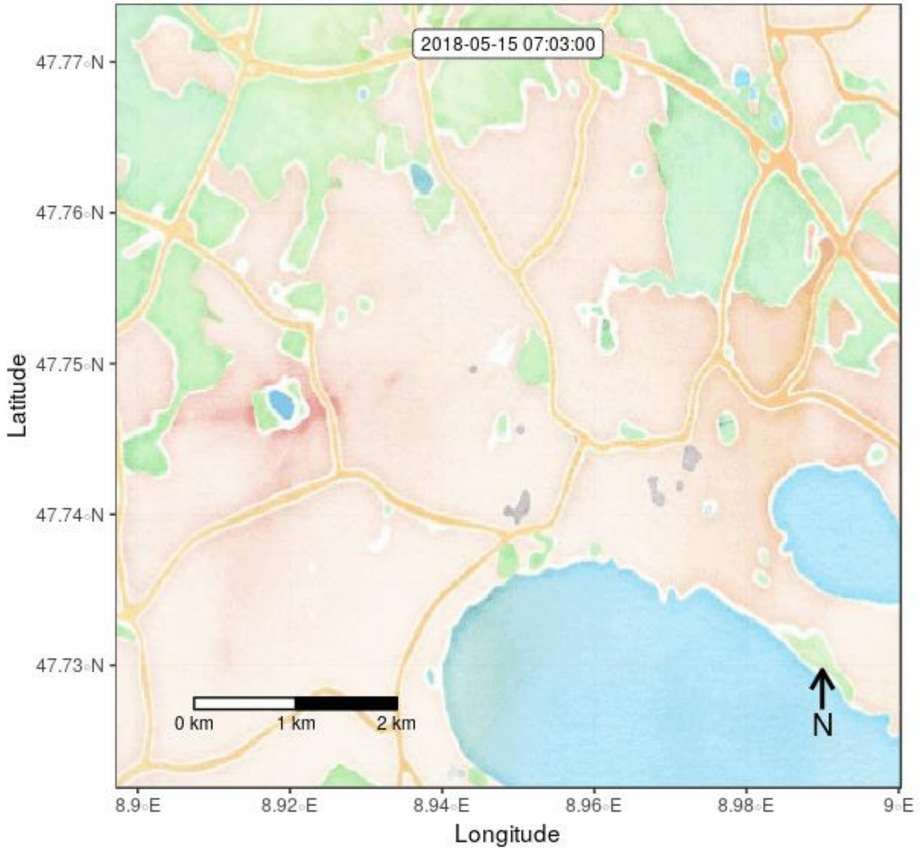
Hawkins (2016)

Fig. Average global temperature from 1850 (left) to 2018 (right)

Animal movement is autocorrelated.

= Violates independence assumptions.

The autocorrelated nature of movement data is ***critical*** to explain animal movement and space-use patterns!

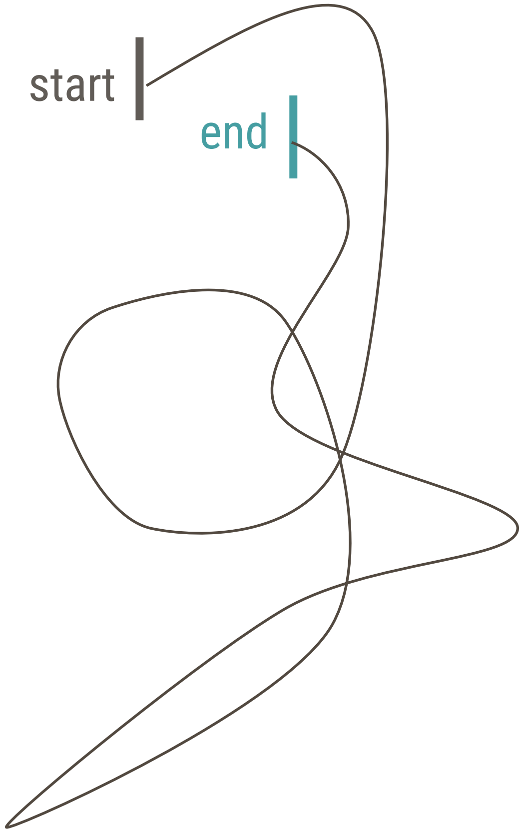


Although animal movement is a continuous process…
Tracking data does not necessarily reflect that.

ANIMAL MOVEMENT $\neq$ TRACKING DATA

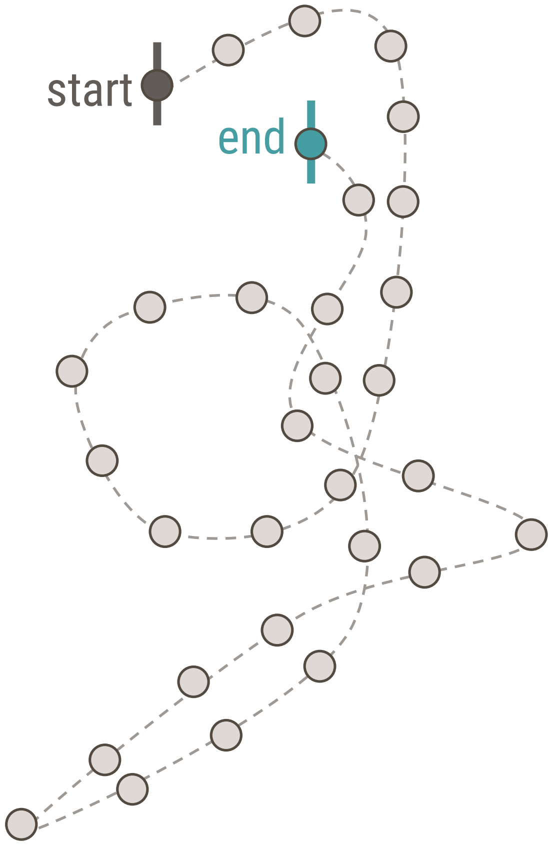
> “Our data is never a perfect reflection of the real world.”

- only a subset: not real movement, only collected locations,
- collected by humans: guesstimation, precision and errors,
- collected by machines: precisions and errors.



Animal movement

CONTINUOUS-TIME PROCESS



Animal movement

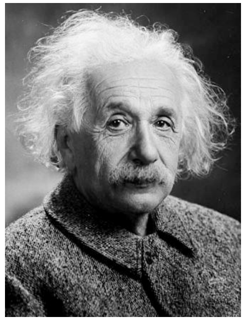
CONTINUOUS-TIME PROCESS

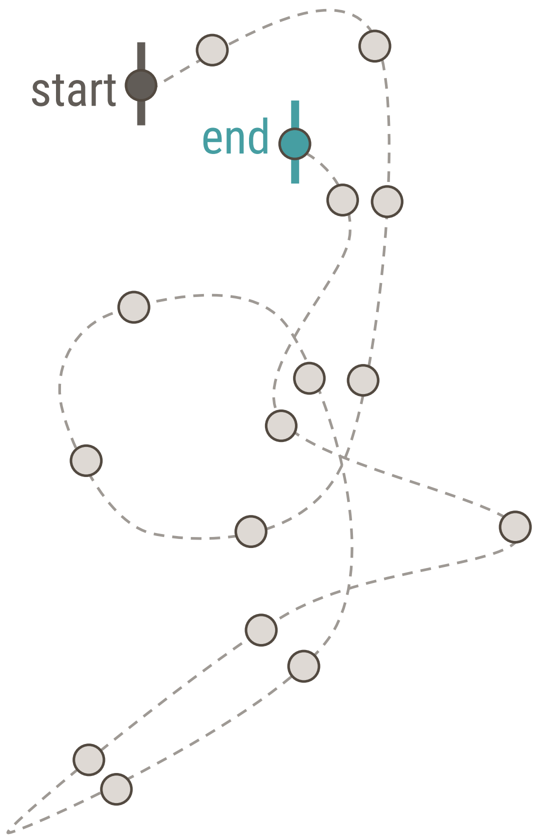
Loss of information

Animal tracking data

DISCRETE-TIME

"
"Everything should be made as simple as possible … but not simpler."





Animal movement

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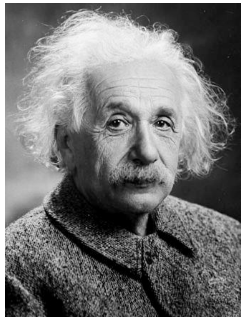

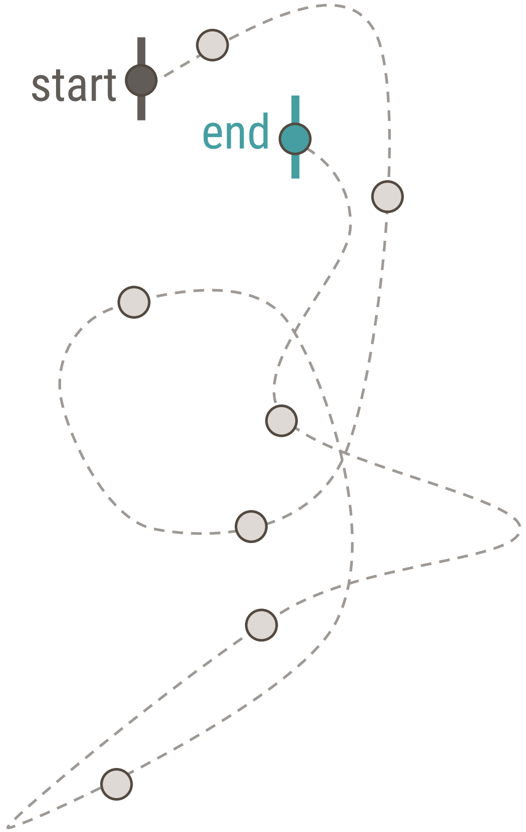

Animal movement

CONTINUOUS-TIME PROCESS

MOVEMENT MODEL

Loss of information

Animal tracking data

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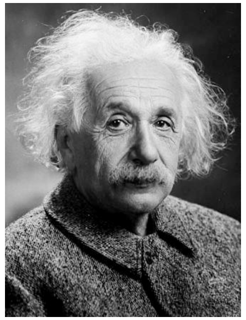

HOME RANGE

First defined in Burt (1943) as:

“the area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional ventures outside the area, perhaps exploratory in nature, should not be considered part of the home range.”

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> “the area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional ventures outside the area, perhaps exploratory in nature, should not be considered part of the home range.”

- How to quantify home range area.

HOME RANGE not actively defended ≠ **TERRITORY** actively defended

First defined in Burt (1943) as:

> “the area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional ventures outside the area, perhaps exploratory in nature, should not be considered part of the home range.”

- What constitutes an exploratory move.
- How to quantify an exploratory move.
- How to define the area from which exploratory moves are made.

In practice, it is hard to define when a move is purely *exploratory*.

Exclusion of infrequent outlying relocation points

UTILIZATION DISTRIBUTION

RANGE DISTRIBUTION

extrapolate space use into the future

"How much space does an animal need over the long term?"

What is an animal's home range area?
What is their the population range are?
Are protected areas sufficiently large?

≠

OCCURRENCE DISTRIBUTION

interpolate between data points in the past

"Where did an animal go during a period of observation?"

Where did an animal cross a linear feature?
How likely is it that it visited a location of interest?
How much time did it spend in a specific habitat?

RStudio®

UTILIZATION DISTRIBUTION

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"How much space does an animal need over the long term?"

What is an animal's home range area?
What is their the population range are?
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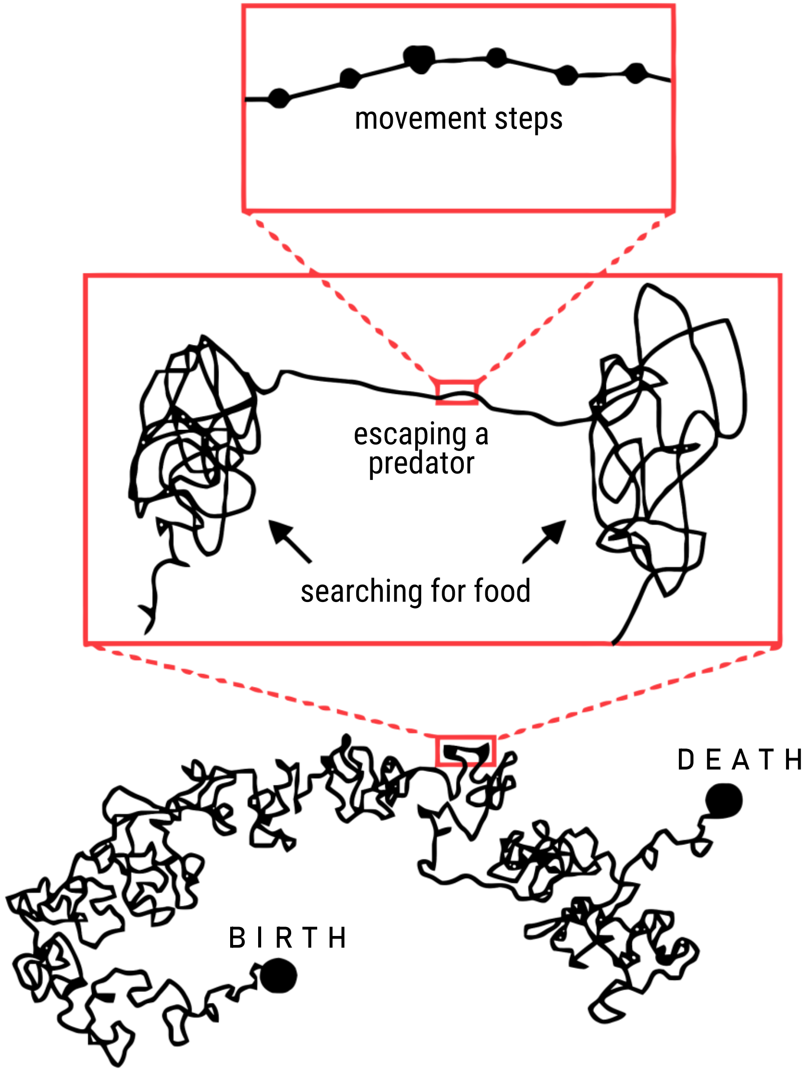
HOME RANGE

Here, we follow the definition of home range as the area repeatedly used throughout an animal's **lifetime** for all its normal behaviors and activities, excluding occasional exploratory excursions.

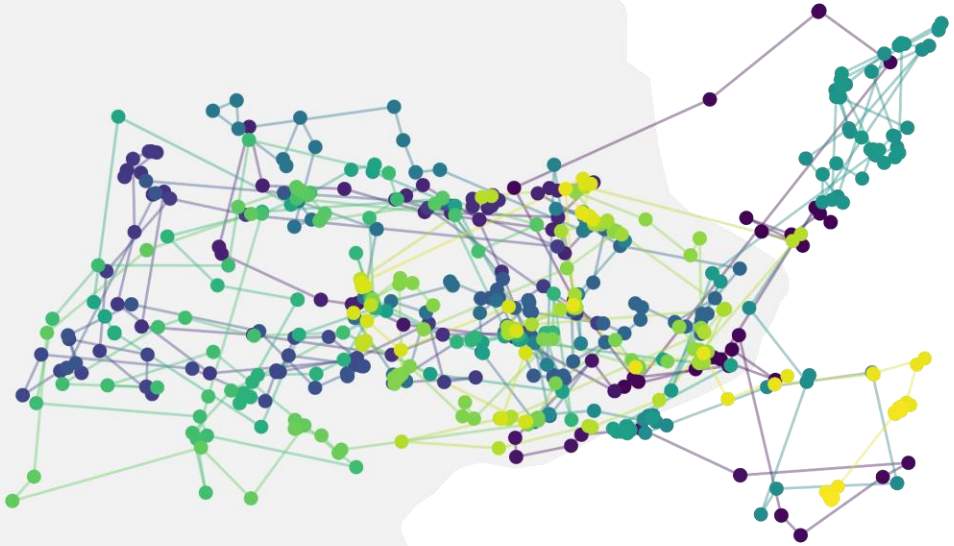
Home range area can be expected to include future locations.



HOME RANGE

It is vital to capture the area repeatedly used throughout an animal's lifetime.

VHF data
Duration: 1 year



PROTECTED AREA UNPROTECTED AREA

Example:

Conservation and management, to understand human-wildlife conflict.

VU

SPECIES
KING COBRA
OPHIOPHAGUS HANNAH

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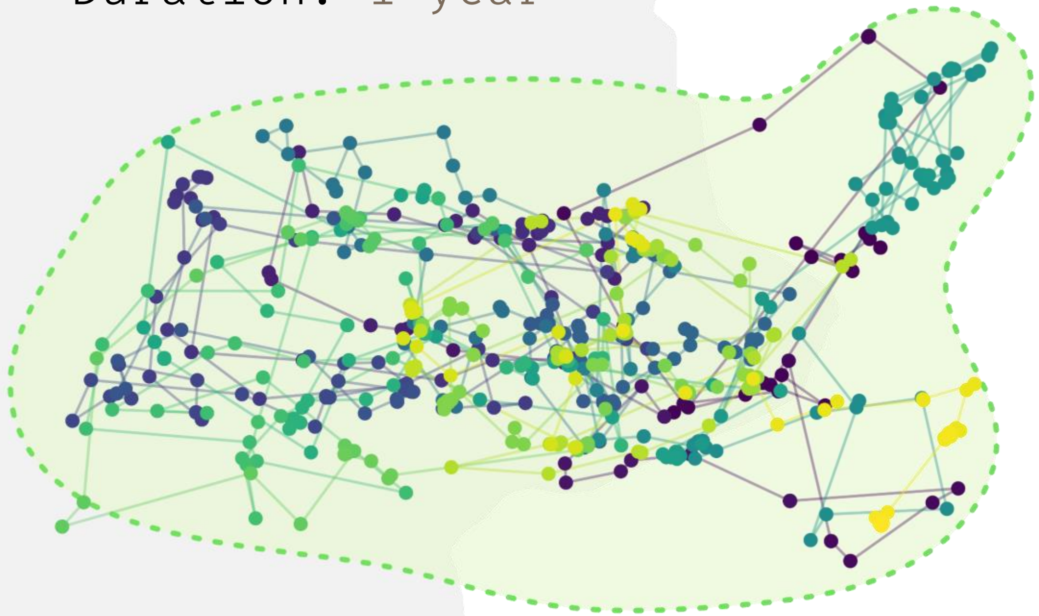

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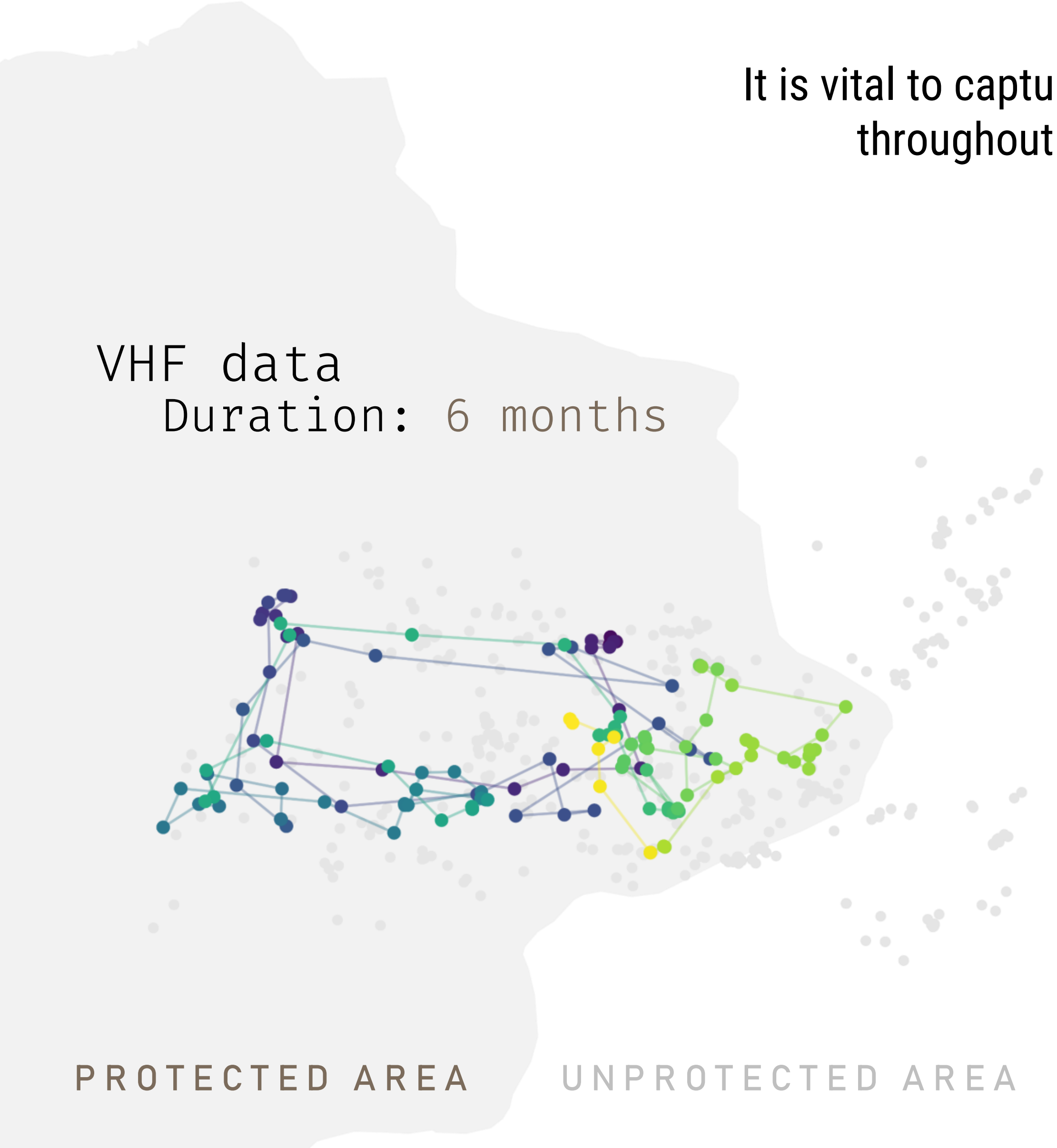

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Conservation and management, to understand human-wildlife conflict.

SPECIES
KING COBRA
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SAMPLE SIZE

It is important to distinguish two sample size concepts:

n

ABSOLUTE
SAMPLE SIZE

SAMPLING DURATION
How long is an animal tracked for?

6 months

SAMPLING FREQUENCY
How frequently are locations collected?

1 fix every 20 minutes

17,520 locations

Total number of locations

SAMPLE SIZE

It is important to distinguish two sample size concepts:

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ABSOLUTE SAMPLE SIZE

SAMPLING DURATION

How long is an animal tracked for?

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17,520 locations

Total number of locations

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EFFECTIVE SAMPLE SIZE

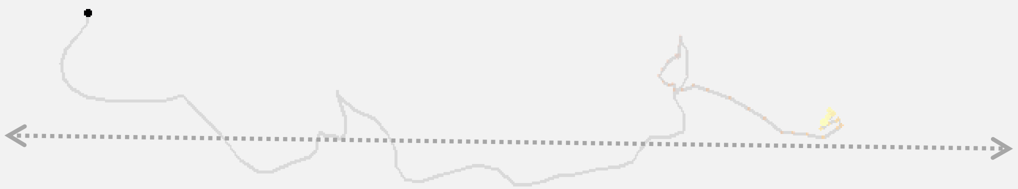
roughly estimated as T/τ_p

T is the sampling duration

τ_p is the average ***home range crossing time***

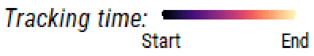
τ_p

HOME RANGE CROSSING TIMESCALE PARAMETER



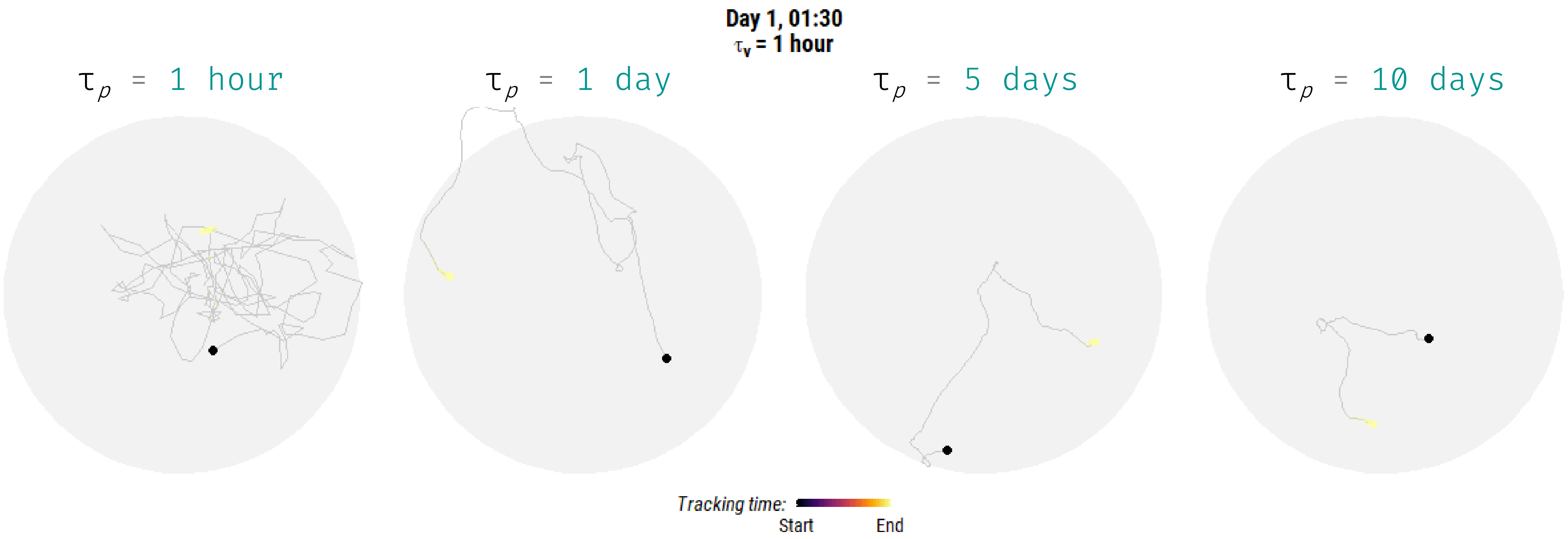
How long does it take for an animal to traverse the linear extent of its home range?

Duration = 1 day
τ_p = 1 day



SAMPLE SIZE

τ_p



Effective sample size **(N) decreases as the *home range crossing time parameter* (τ_p) increases.**

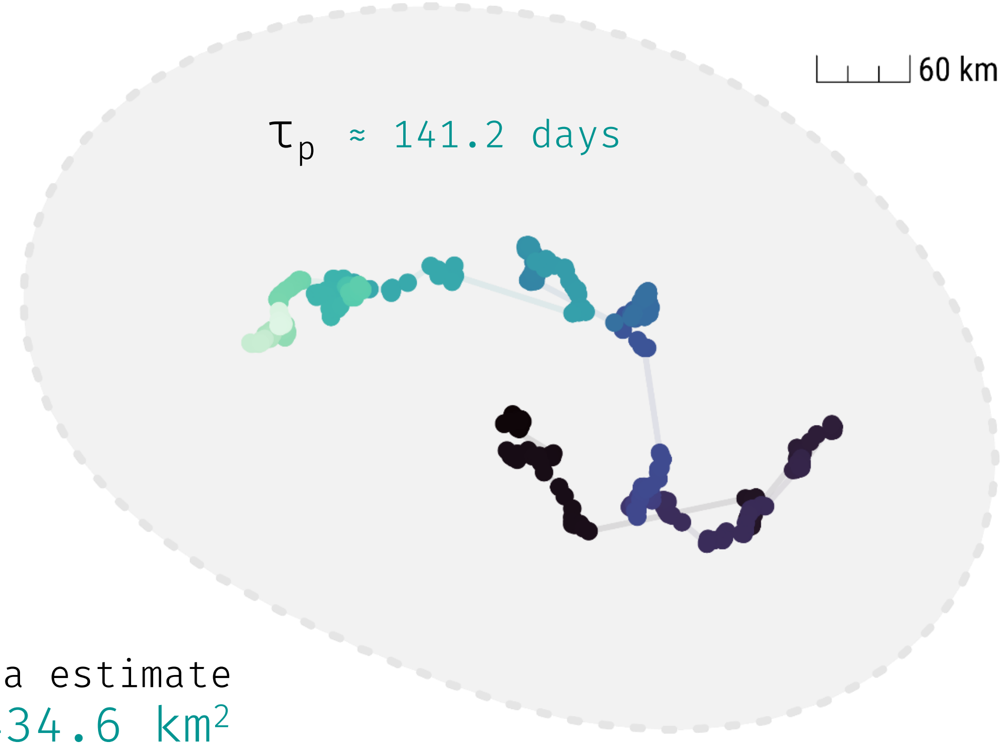
SAMPLE SIZE

MONGOLIAN GAZELLE

PROCOPRA GUTTUROSA

Sampling duration = tracked for 389 days

Sampling frequency ≈ 1 fix every 5 hours



Absolute sample size n = 710 locations

Effective sample size N ≈ 2.7 locations

Home range area estimate

303,434.6 km^2

SAMPLE SIZE

For independent data,

$$n = N$$

For autocorrelated data,

$$n \gg N$$

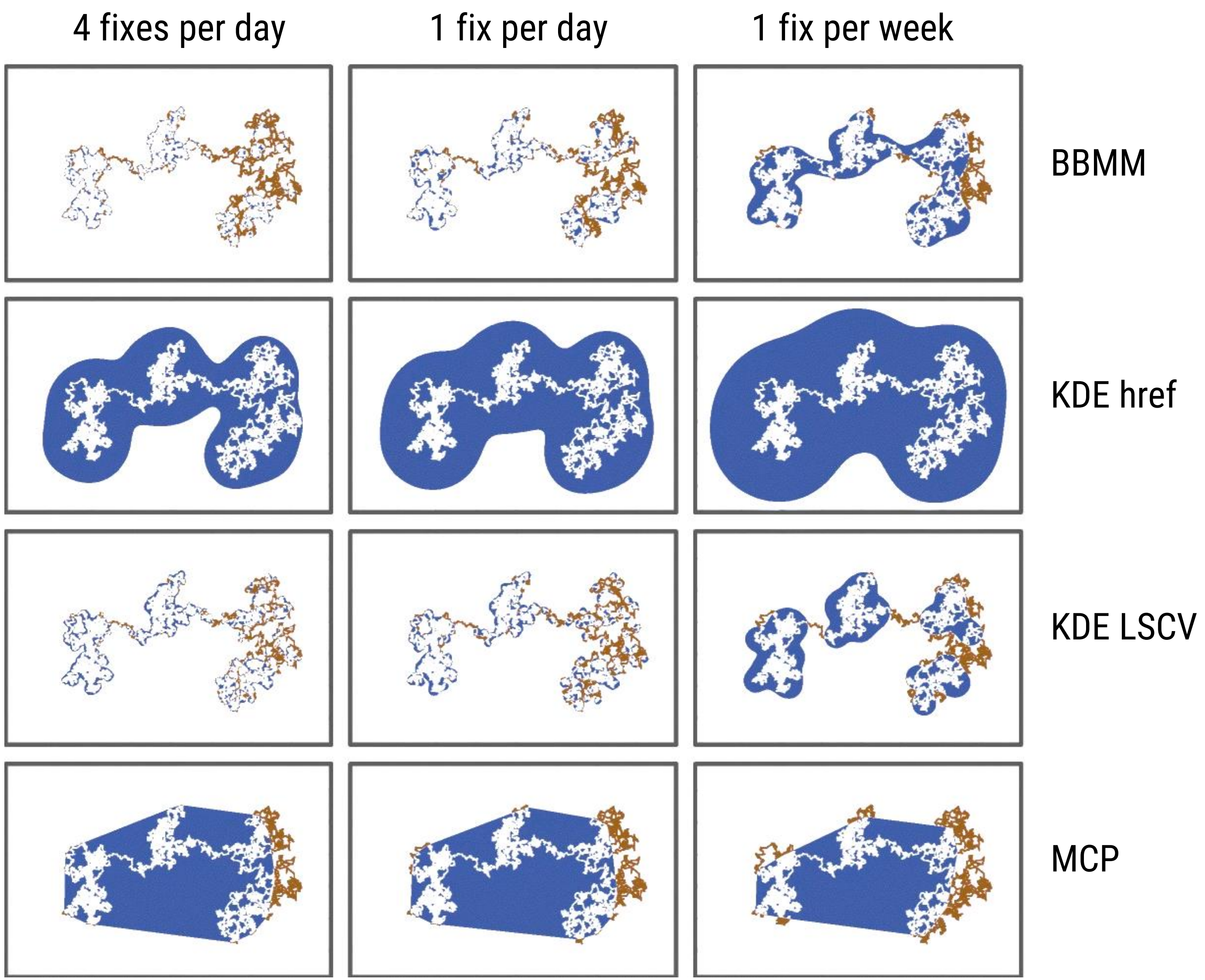
n = absolute sample size
N = effective sample size

Many biases, including most that affect home range estimation, are exacerbated by small sample sizes.

ESTIMATORS

One of the primary reasons for collecting animal movement data is home range estimation.

However, not all methods are appropriate …



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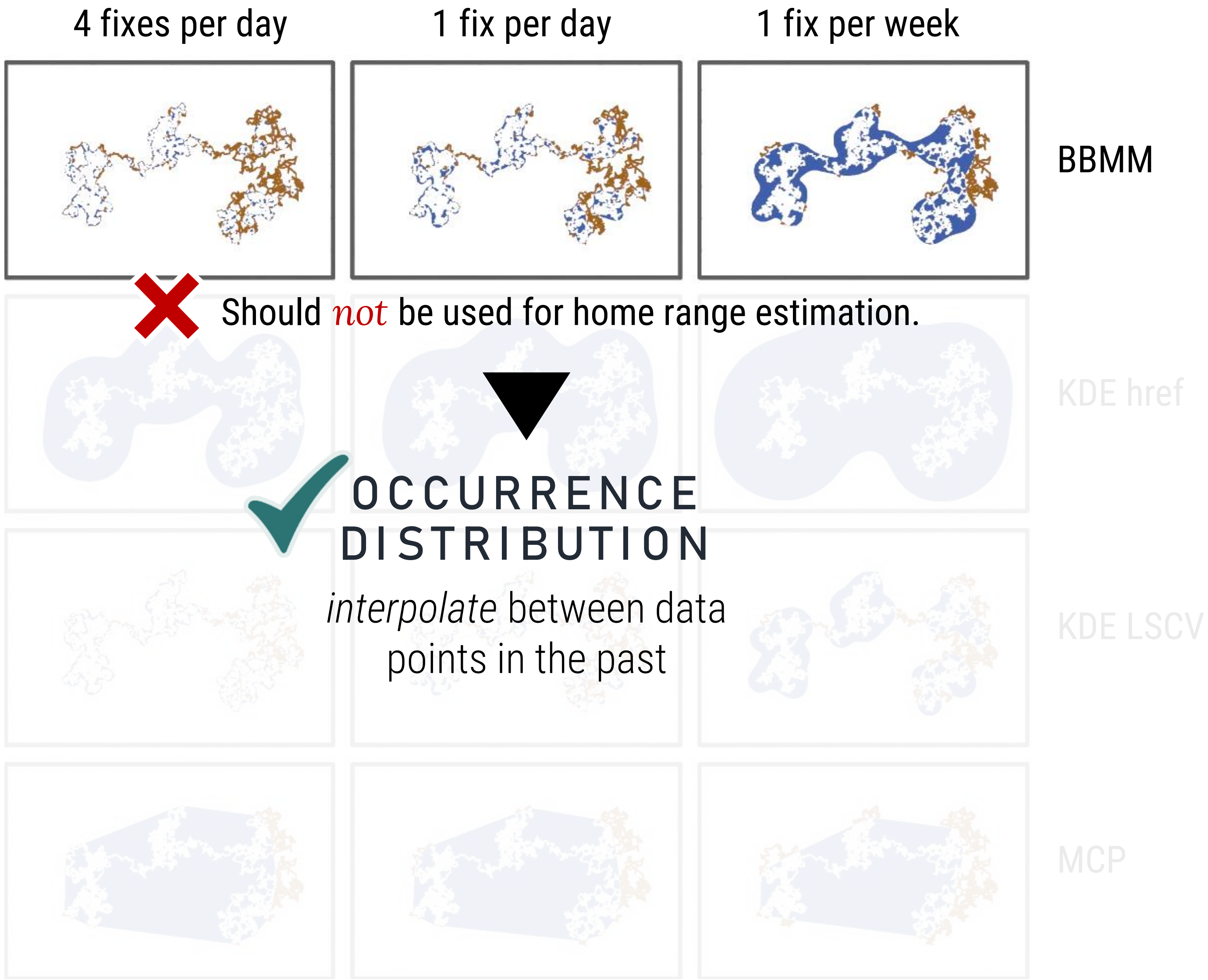

Should *not* be used for home range estimation.

OCCURRENCE DISTRIBUTION

interpolate between data points in the past

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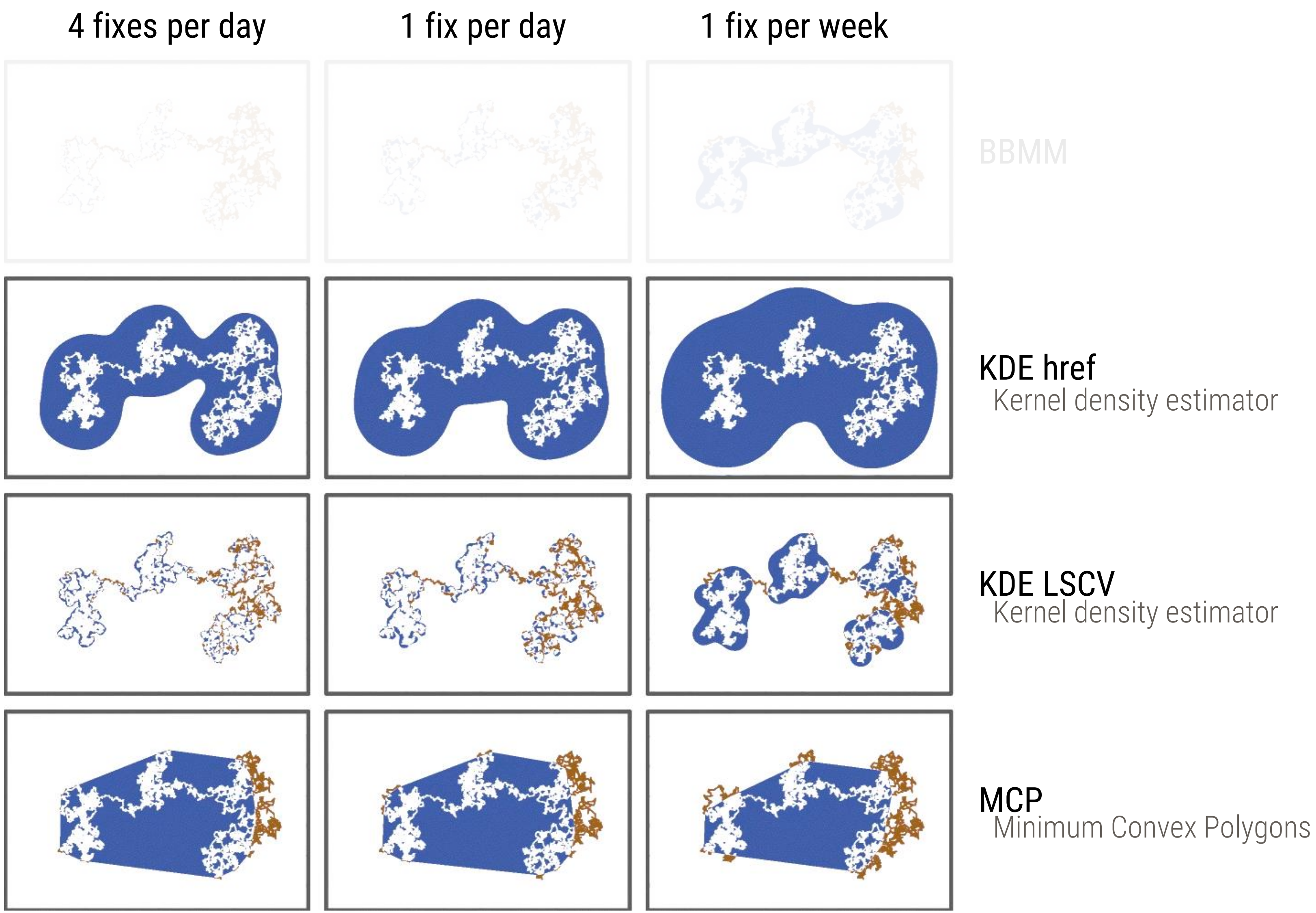


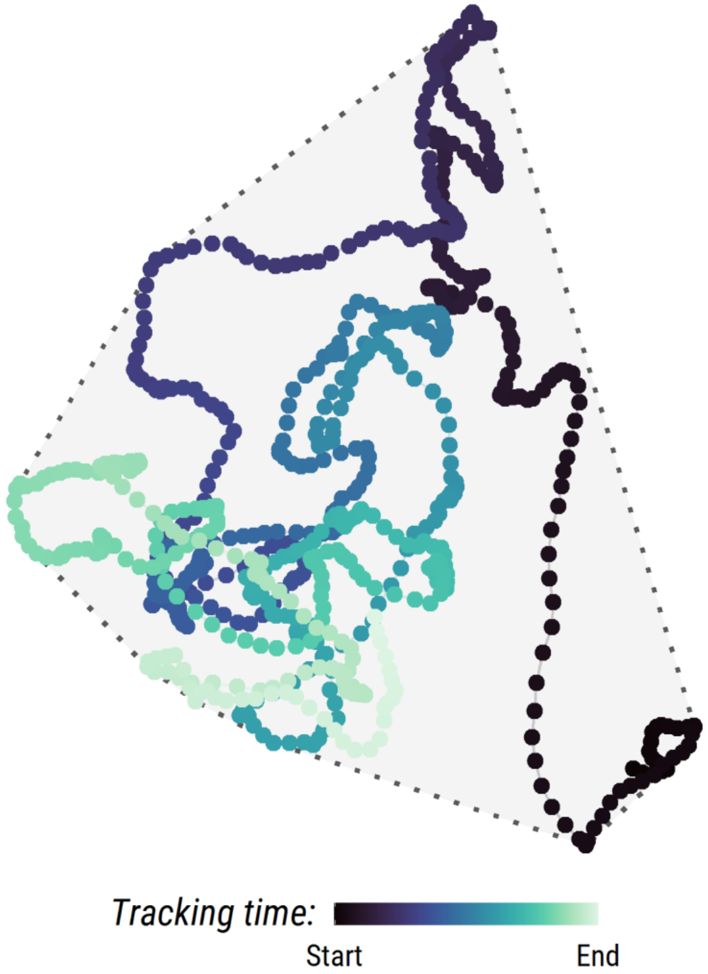
Minimum Convex Polygon (MCP)

Kernel density estimator (KDE)

Minimum Convex Polygon (MCP)

Kernel density estimator (KDE)

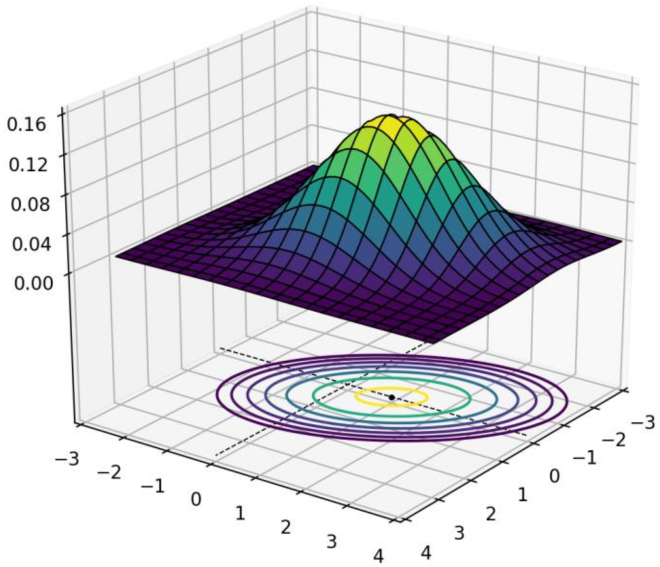
- Assumes uniform use,
- Assumes locations are *independent*;
- Sensitive to *outliers* and point geometry.

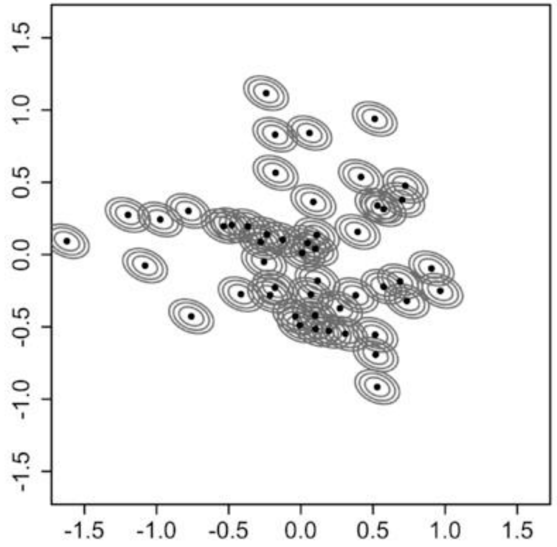


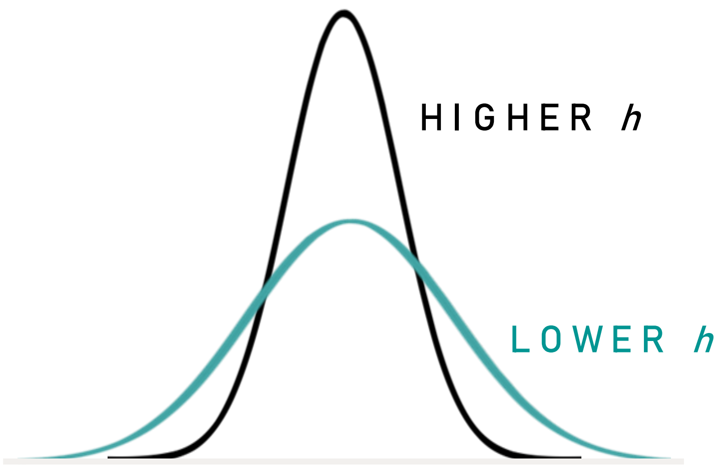
Minimum Convex Polygon (MCP)

Kernel density estimator (KDE)

Kernel density estimates describe not just the borders of the home range, but the probability of use.





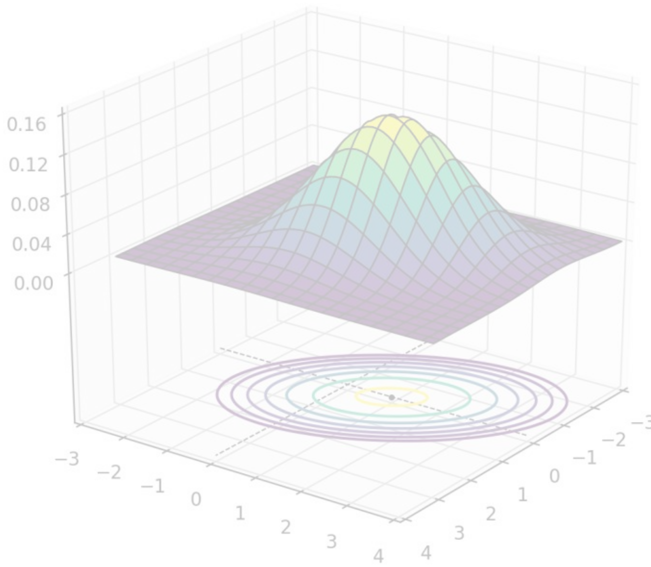


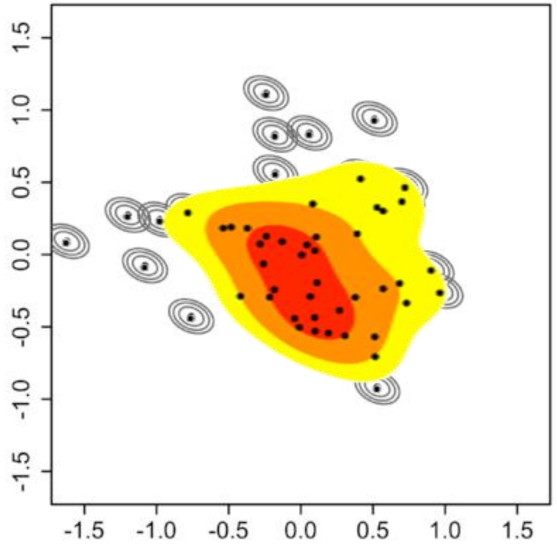
On an x—y plane, each location has a three-dimensional "hill", the kernel.
The shape and width of the kernel, called the ***bandwidth*** (*h*),
can be selected using algorithms.

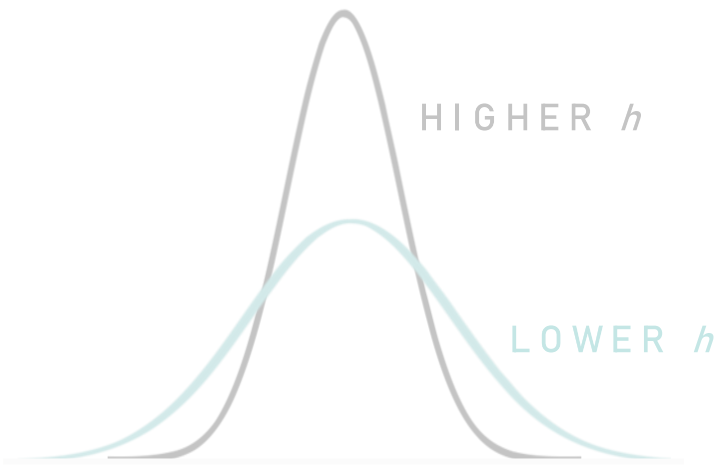
Minimum Convex Polygon (MCP)

Kernel density estimator (KDE)

Kernel density estimates describe not just the borders of the home range, but the probability of use.



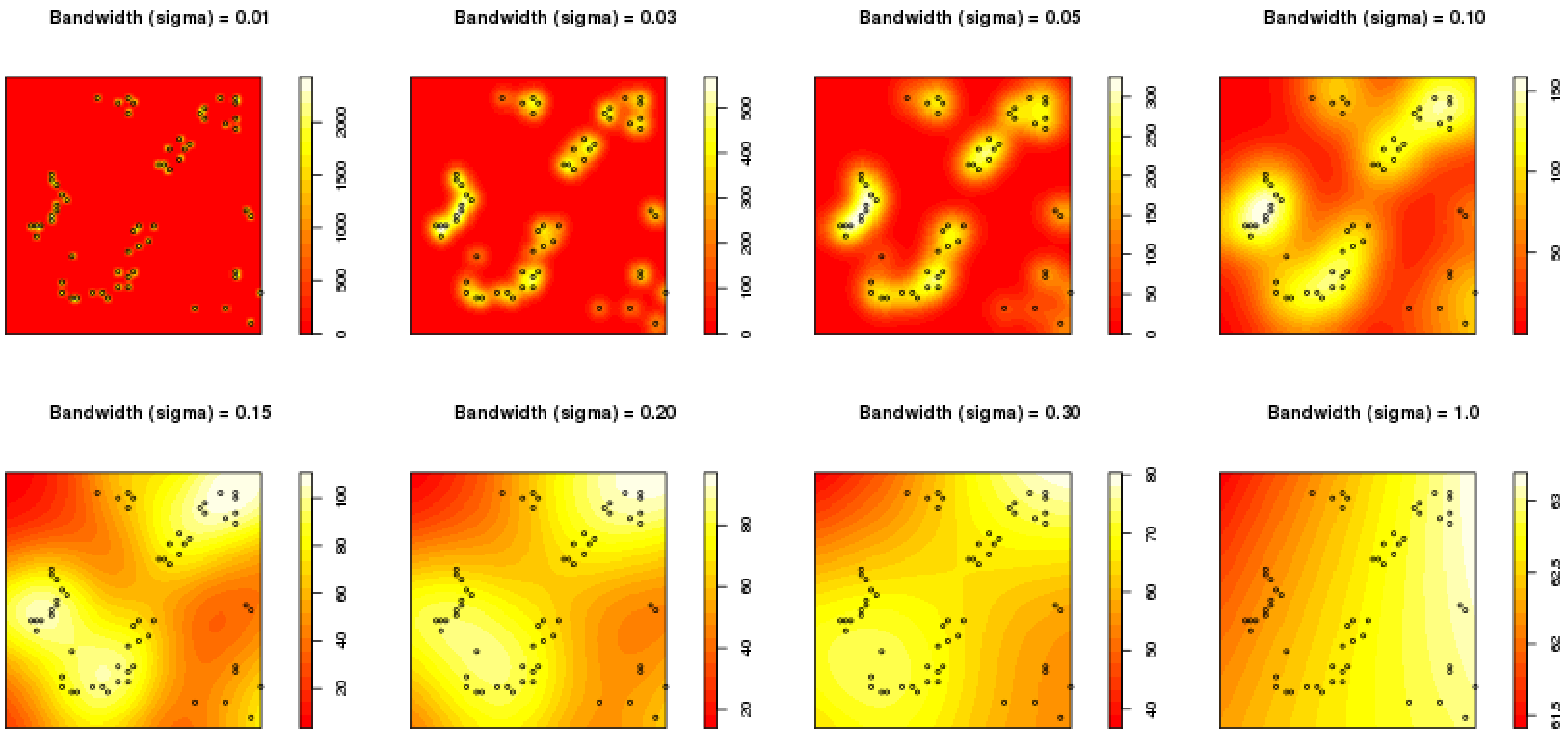




These kernels are then averaged, showing an ***estimate*** of the underlying distribution of all locations.

Minimum Convex Polygon (MCP)

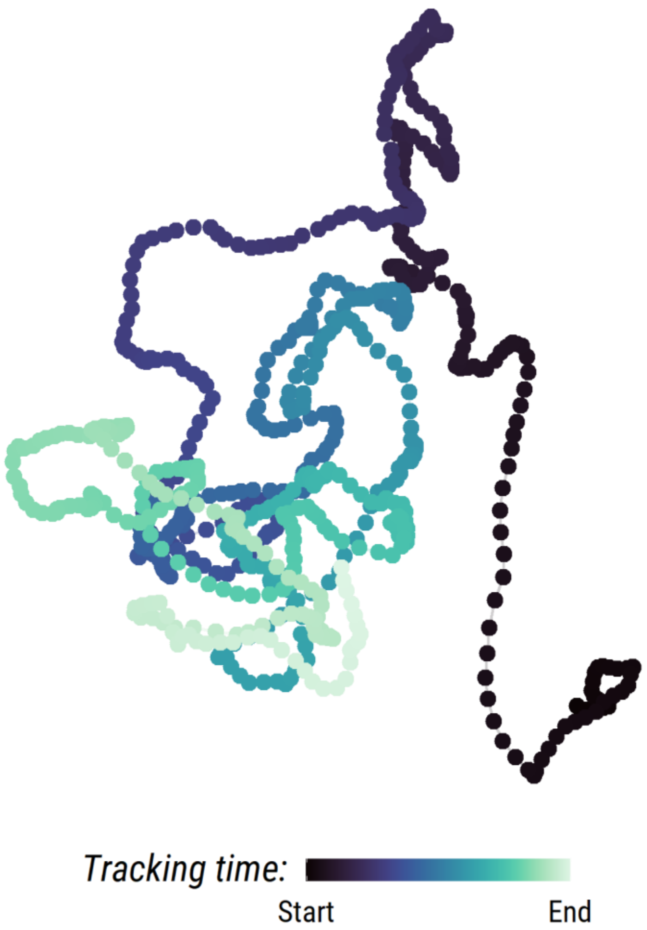
Kernel density estimator (KDE)



bandwidth (*h*), or *smoothing parameter*

Minimum Convex Polygon (MCP)

Kernel density estimator (KDE)

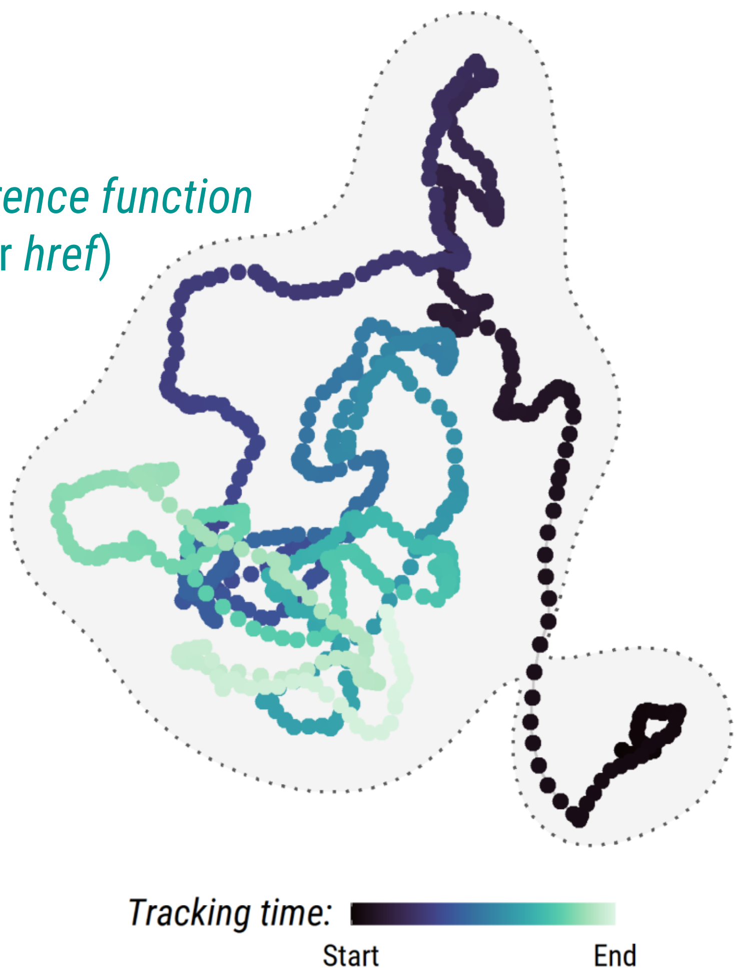


Minimum Convex Polygon (MCP)

Kernel density estimator (KDE)

Gaussian reference function
(GFR or *href*)

- Assumes locations are *independent*;
- Sensitive to *bandwidth selection*.



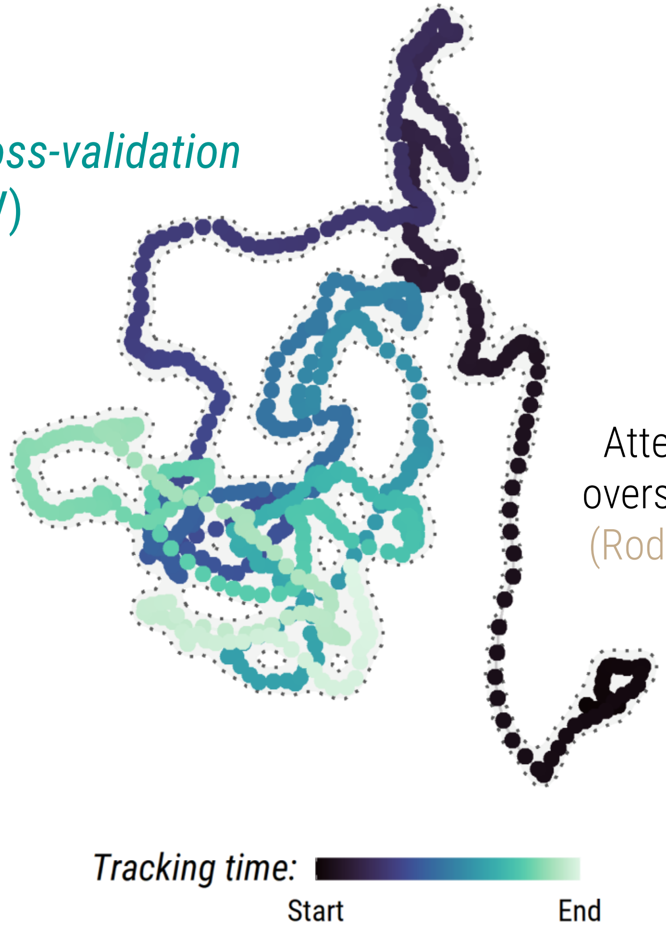
Minimum Convex Polygon (MCP)

Kernel density estimator (KDE)

Least-squares cross-validation
(LSCV)

- Assumes locations are *independent*;
- Sensitive to *bandwidth selection*.

This algorithm performs poorly with **large sample sizes**, and still does not account for the locations' temporal structure.



Attempts to prevent oversmoothing of KDE (Rodgers & Kie, 2010)

Thinning the data….

Fig. Tracking data representing ***hourly locations*** over ***one month.***

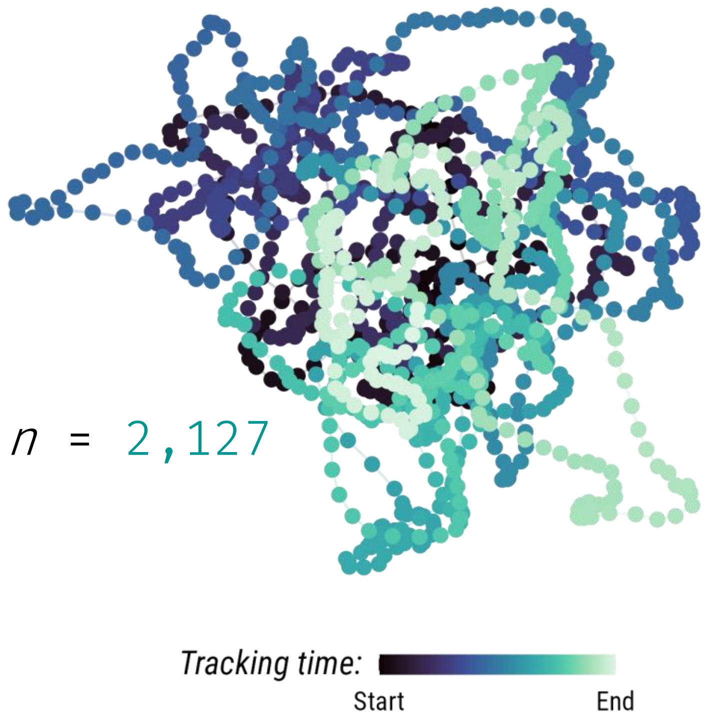
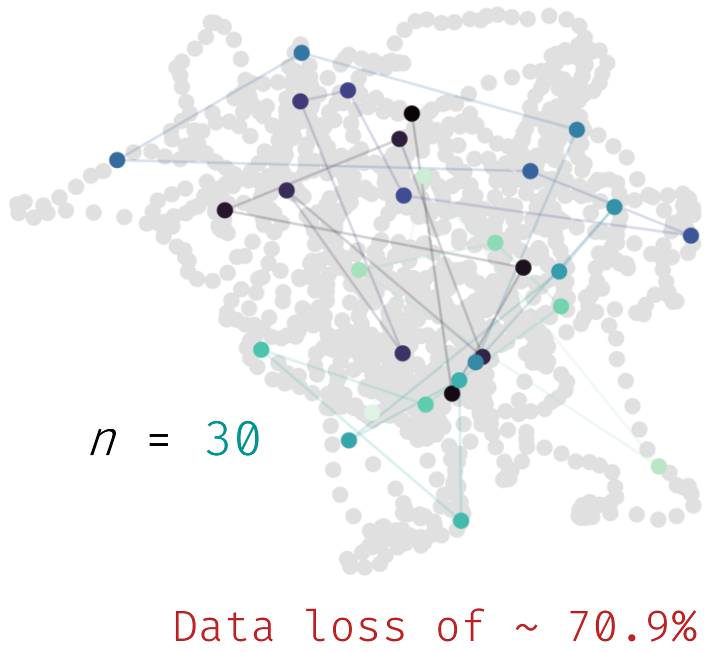


Fig. Tracking data subsampled so there is only ***one location per day***.



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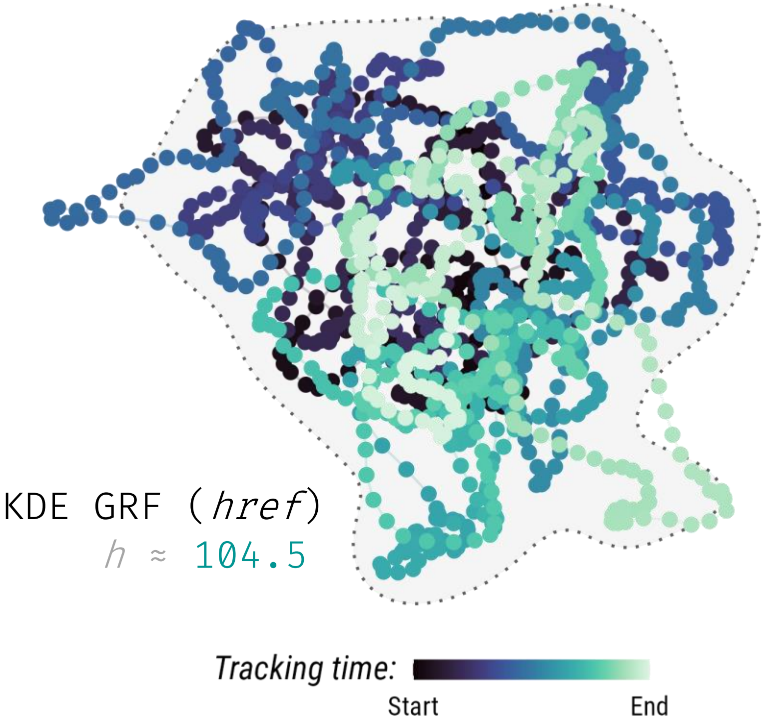

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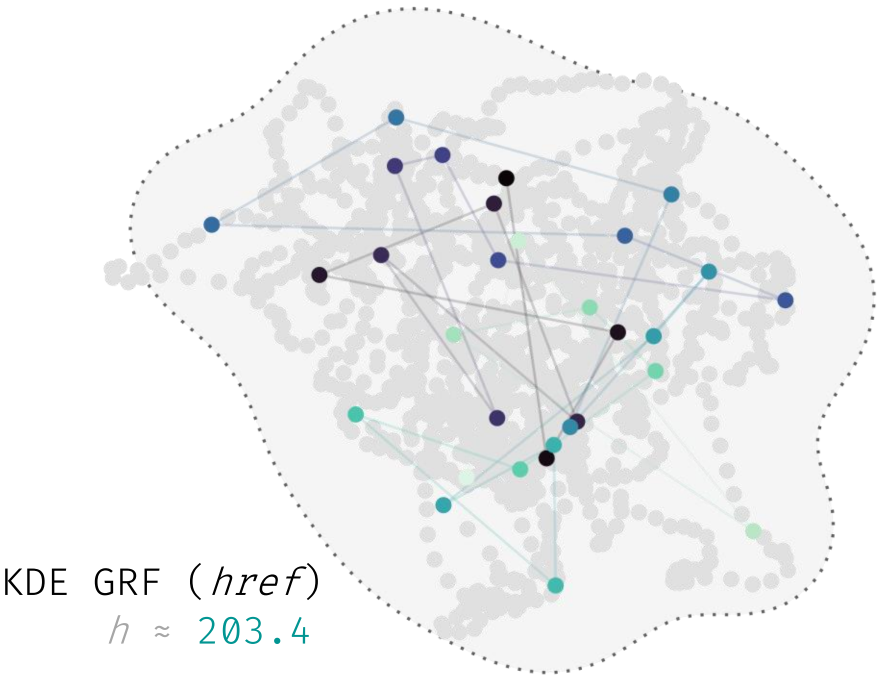

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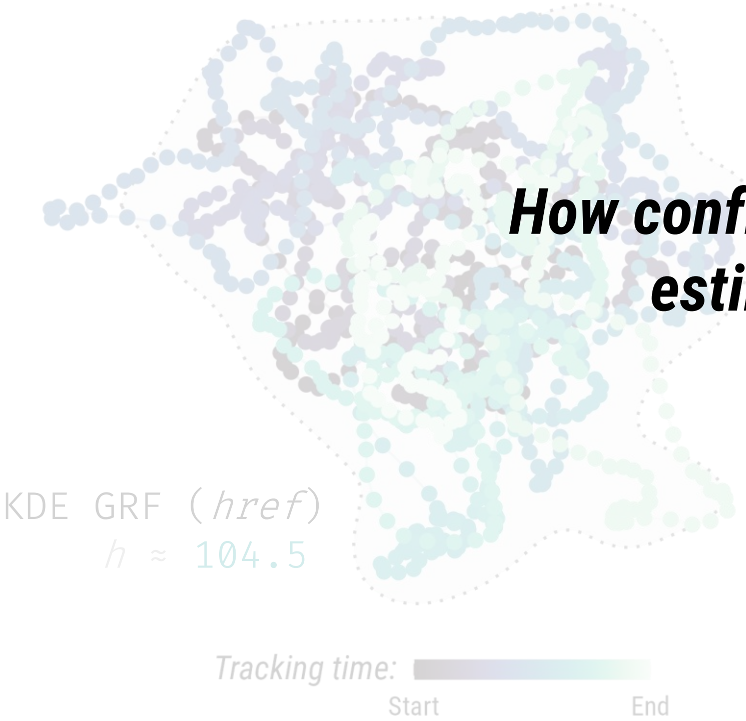
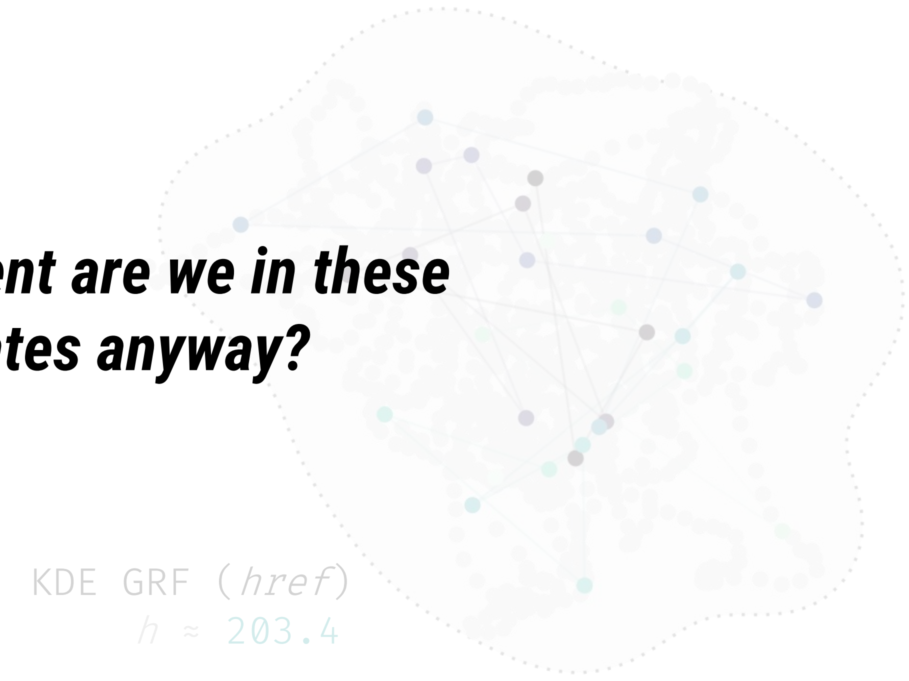
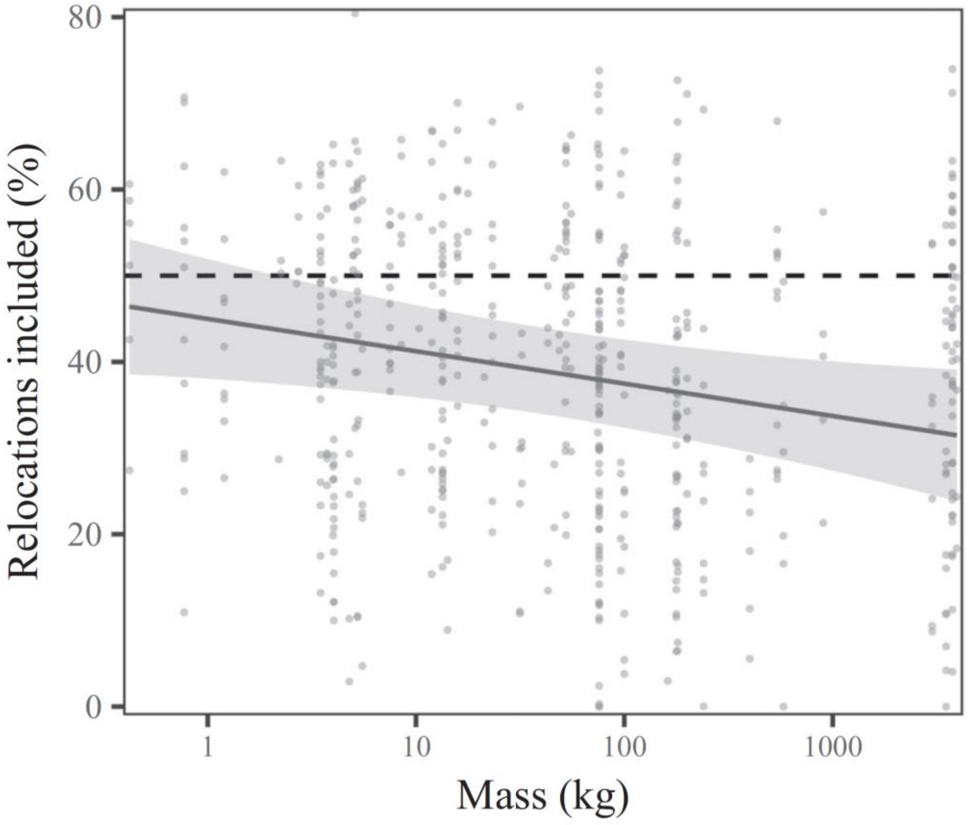


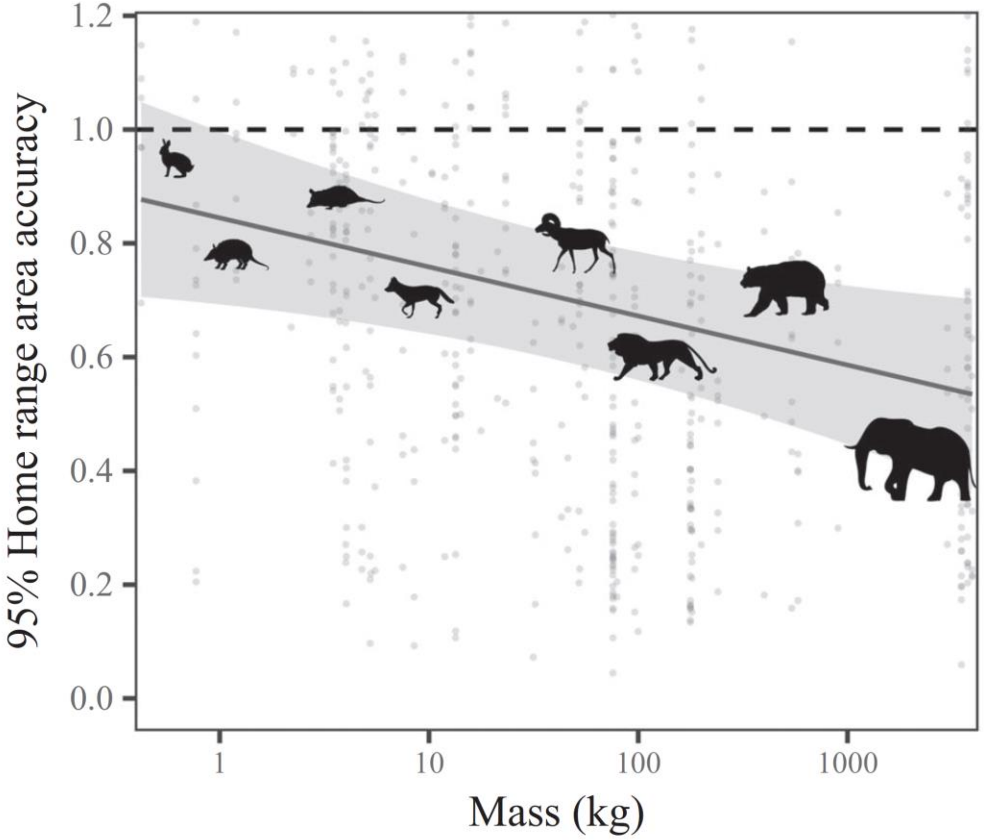


How confident are we in these estimates anyway?

Kernel density estimator (KDE)

The magnitude of KDE's underestimation worsened as body mass increased.

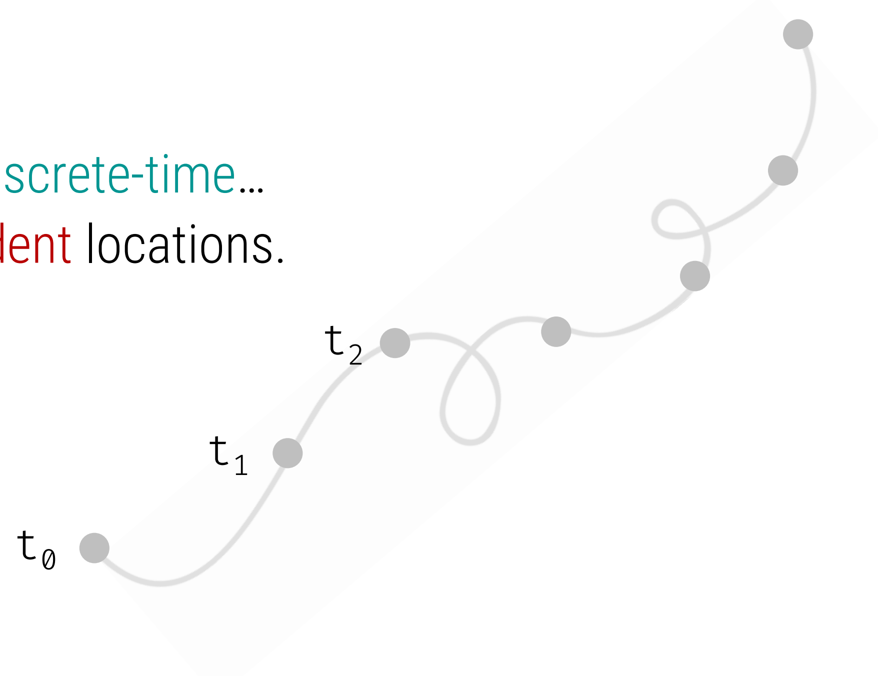




ESTIMATORS

Assuming discrete-time…
…and independent locations.

Discrete-time models are
also scale-dependent.



Sampling may be irregular in time,
and sampling schedules may differ across individuals.

Assuming discrete-time…
…and independent locations.

Discrete-time models are also scale-dependent.

By considering continuous-time movement models!

Sampling may be irregular in time,
and sampling schedules may differ across individuals.

How do we fix this?

`{ctmm} R package:` Functions for identifying, fitting, and applying continuous-space, continuous-time stochastic movement models to animal tracking data.

WORKFLOW:

01 Range residency assumption

Checking if data is from a range-resident animal

02 Movement models

Selecting the best-fit movement model through model selection

03 Home range estimation

Reconstructing the range distribution from sampled locations

04 Mitigation measures

Accounting for common biases in animal movement data

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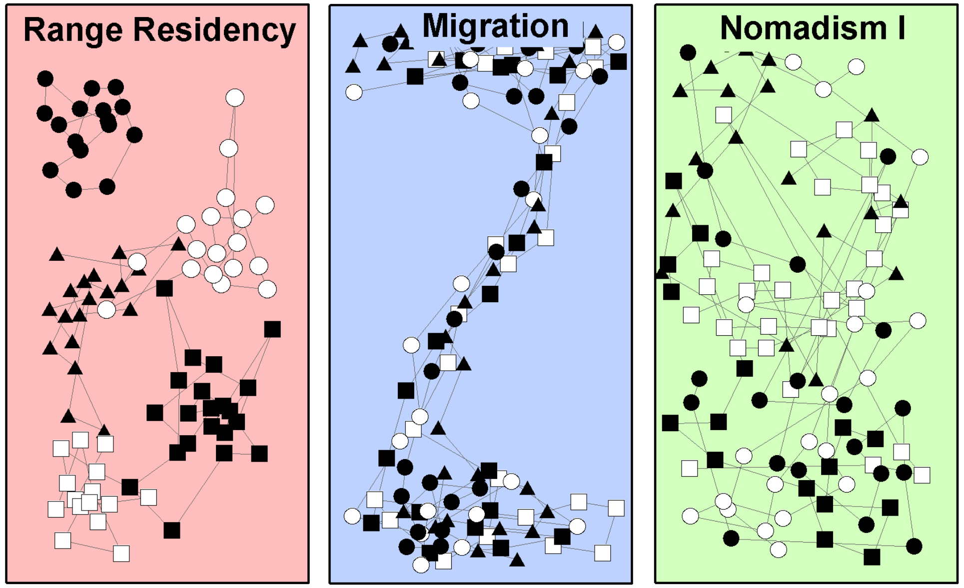
RANGE RESIDENCY

There are three different behaviors that animals exhibit:

- Resident – individual occupies the same area throughout its lifetime.
- Migratory – regular movement to and from spatially disjoint ranges.
- Nomadic – does not follow regular temporal and spatial patterns.



Mueller *et al.* (2008)

DOI: 10.1111/j.0030-1299.2008.16291.x

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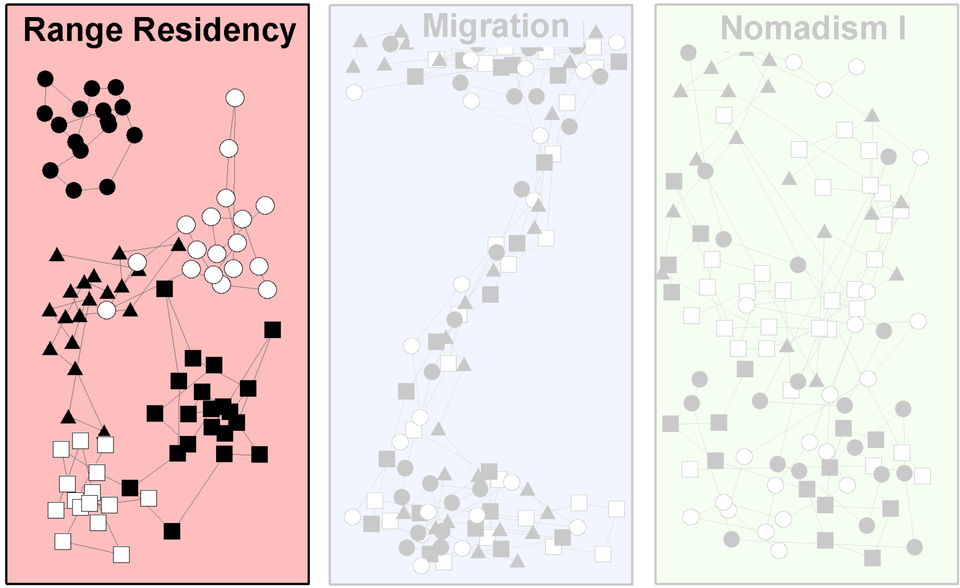

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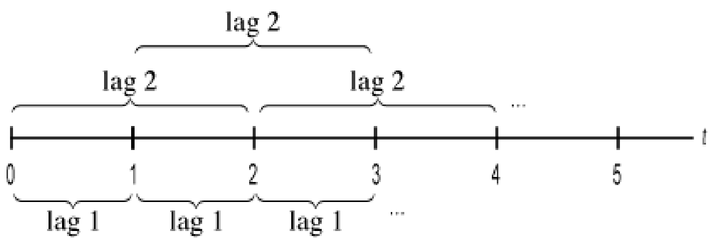
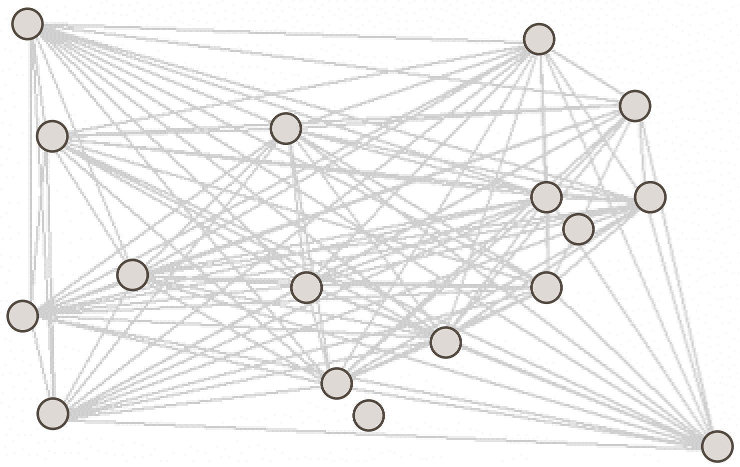
RANGE RESIDENCY

How can we measure and visualize autocorrelation?

Variogram, or *semivariogram*, plots time lags on the x-axis for all pairs of observations against their *semi-variance* (half of the variance for the distance each observation pair) on the y-axis.

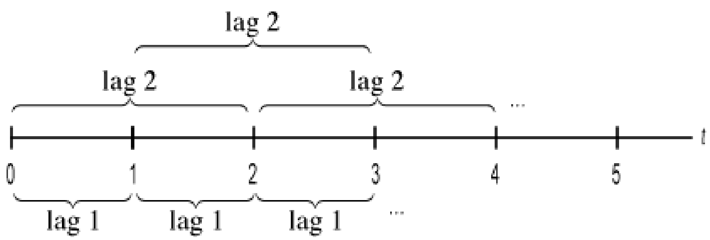




The more **similar** the pairs of locations are per lag, the **lower** the **semivariance** for that lag.

How can we measure and visualize autocorrelation?

Variogram, or *semivariogram*, plots time lags on the x-axis for all pairs of observations against their *semi-variance* (half of the variance for the distance each observation pair) on the y-axis.



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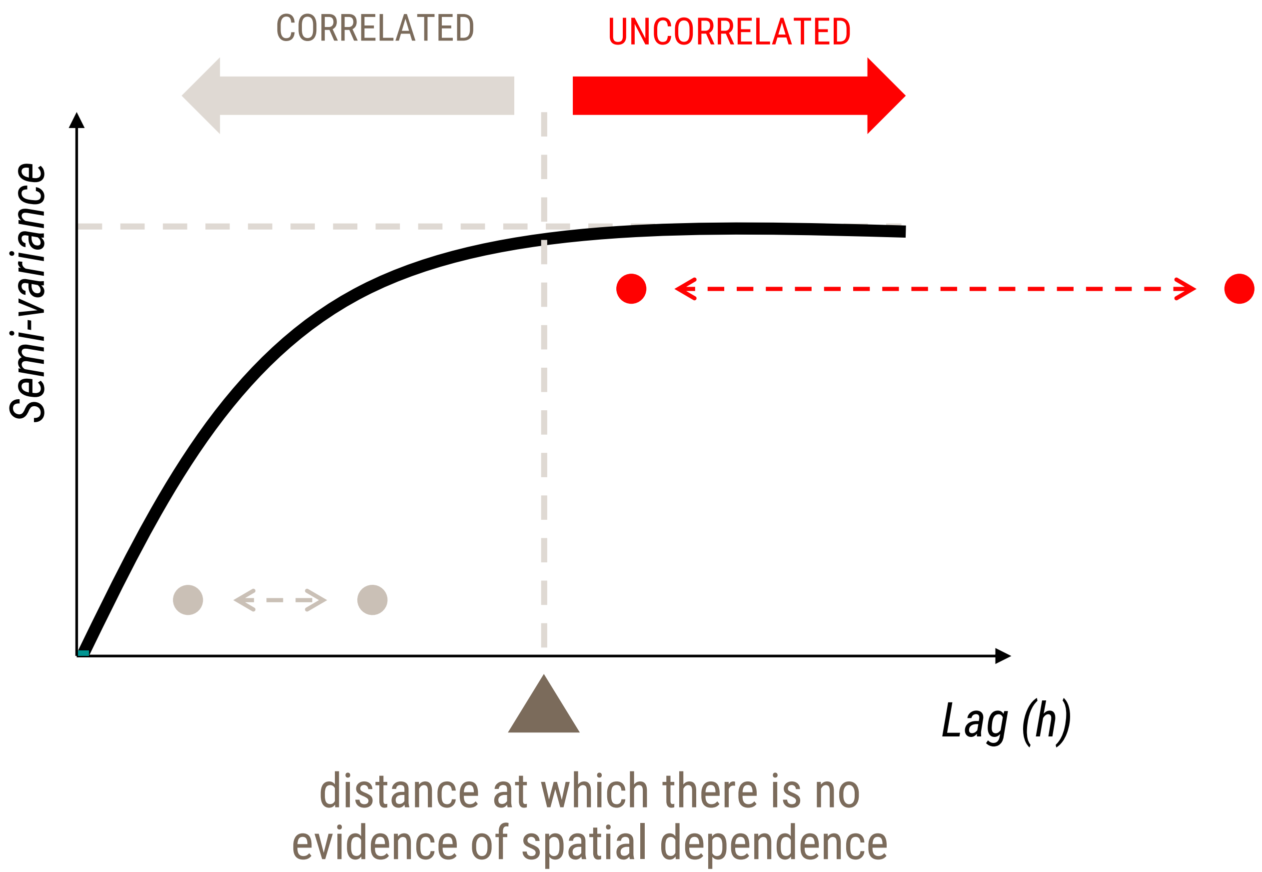

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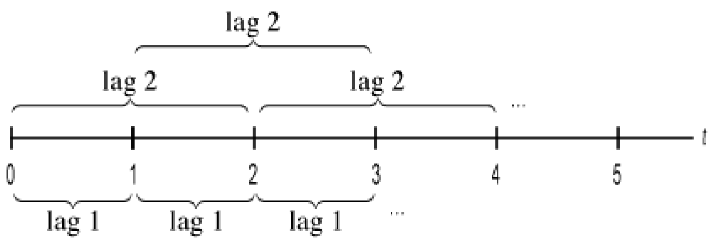

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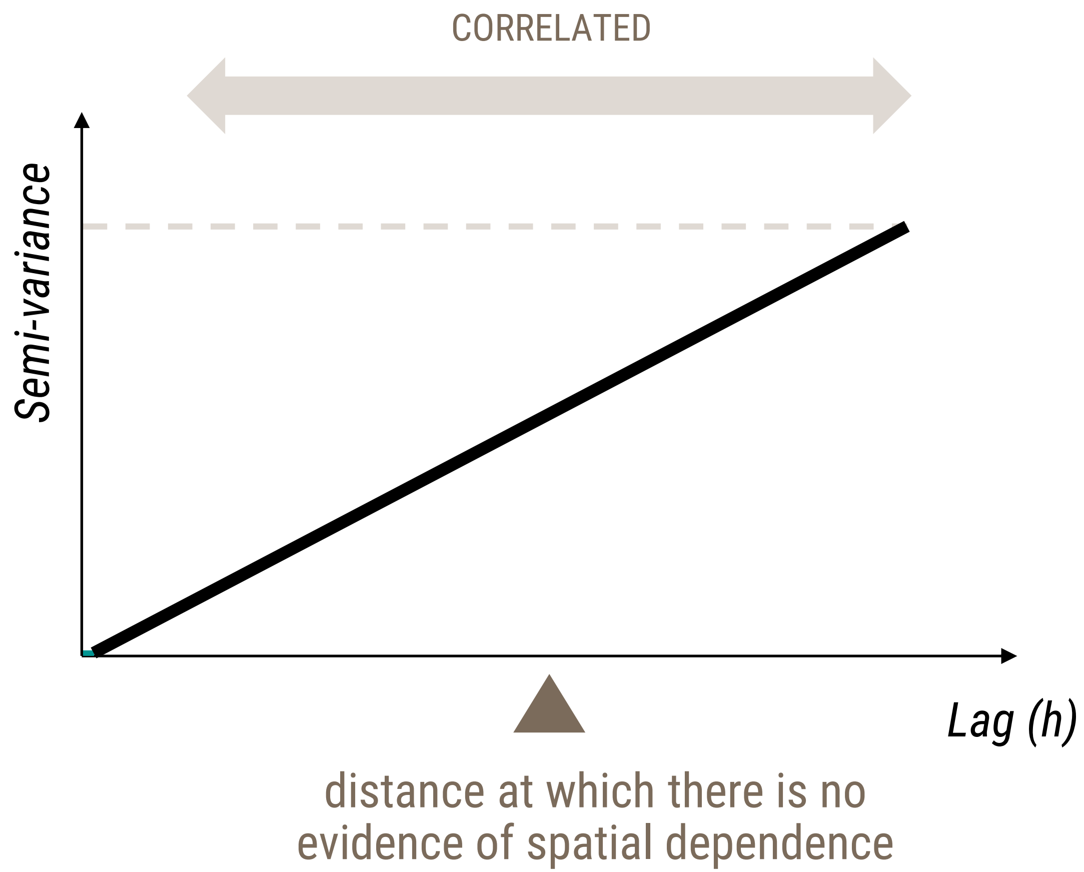
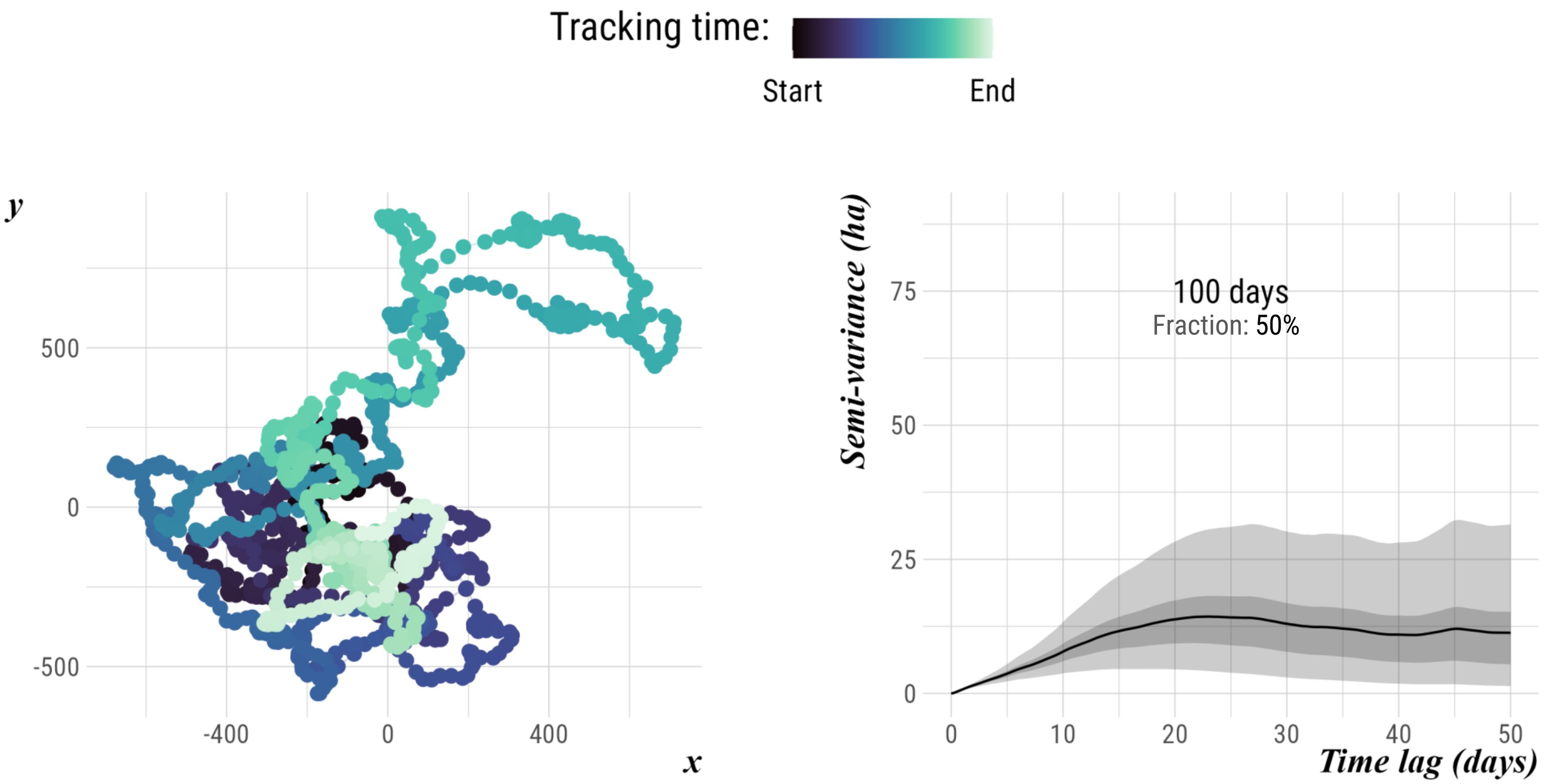


STEP 1

RANGE RESIDENCY



WORKFLOW:

01 **Range residency assumption**

Checking if data is from a range-resident animal

02 **Movement models**

Selecting the best-fit movement model through model selection

03 **Home range estimation**

Reconstructing range distribution from sampled locations

04 **Mitigation measures**

Accounting for common biases in animal movement data

CONVENTIONAL METHODS:

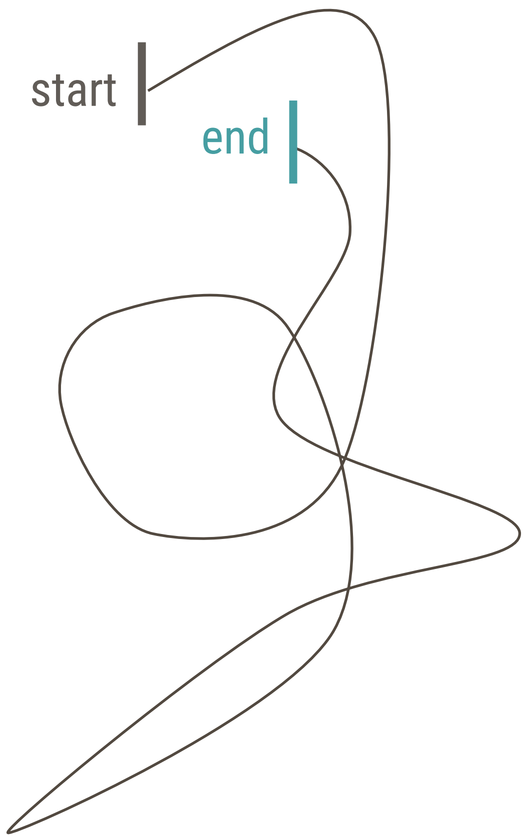
Tracking data → Estimate home range

Assuming *independent locations*.

CTMM R PACKAGE:

Tracking data → Fit movement model → Estimate home range

What *process* explains a particular animal movement dataset?



MOVEMENT MODELS:

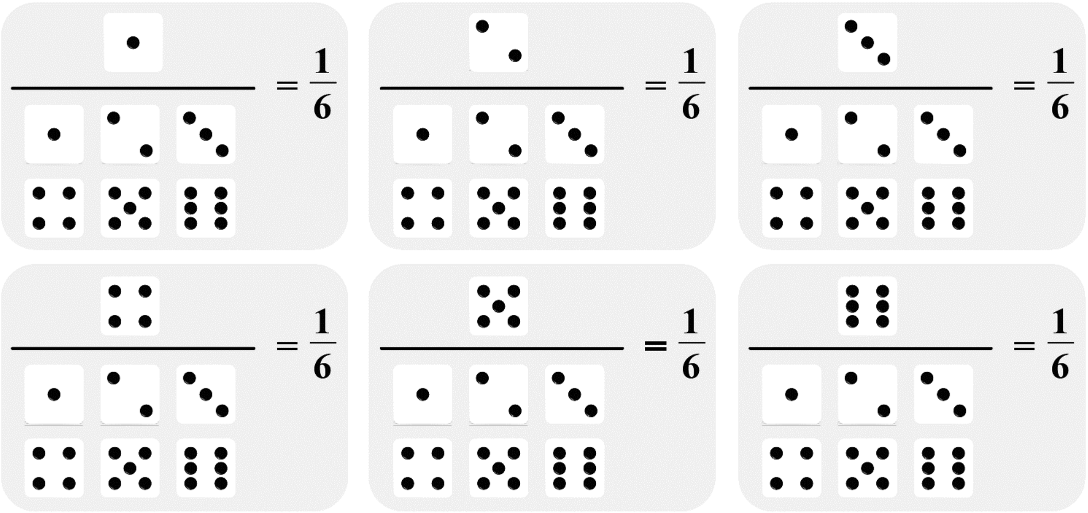
3.1. Independent and Identically Distributed (IID)
3.2. Brownian Motion (BM)
3.3. Ornstein-Uhlenbeck (OU)
3.4. Integrated Ornstein-Uhlenbeck (IOU)
3.5. Ornstein-Uhlenbeck with Foraging (OUF)

3.1. Independent and Identically Distributed (IID)

▼

Stochastic process where each location has the same probability distribution as all others, and all are mutually independent.

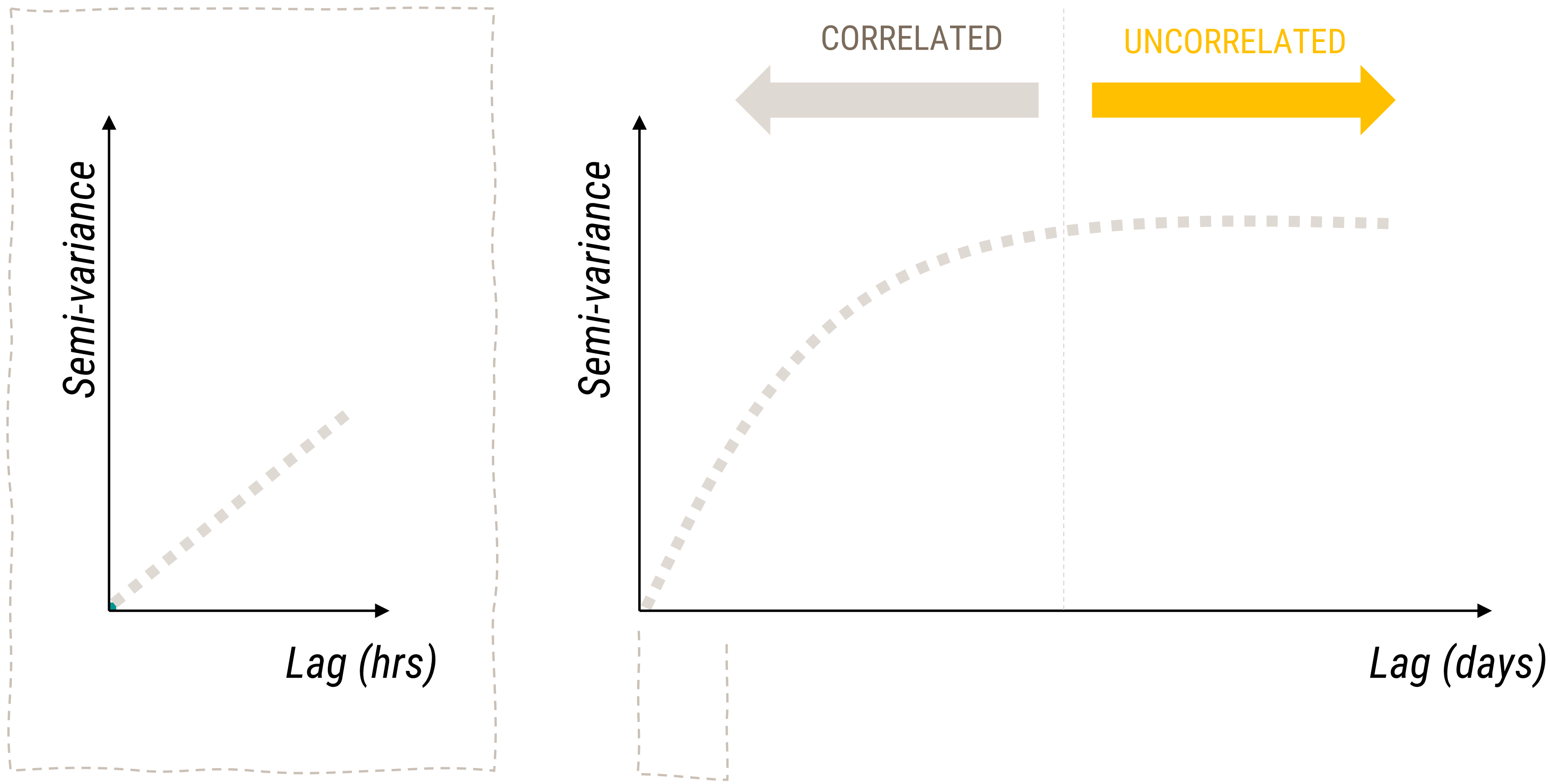
SPATIAL DEPENDENCY
TEMPORAL DEPENDENCY
RESTRICTED



For example,

Dice rolls are ***independent and identically distributed*** (IID)

3.1. Independent and Identically Distributed (IID)



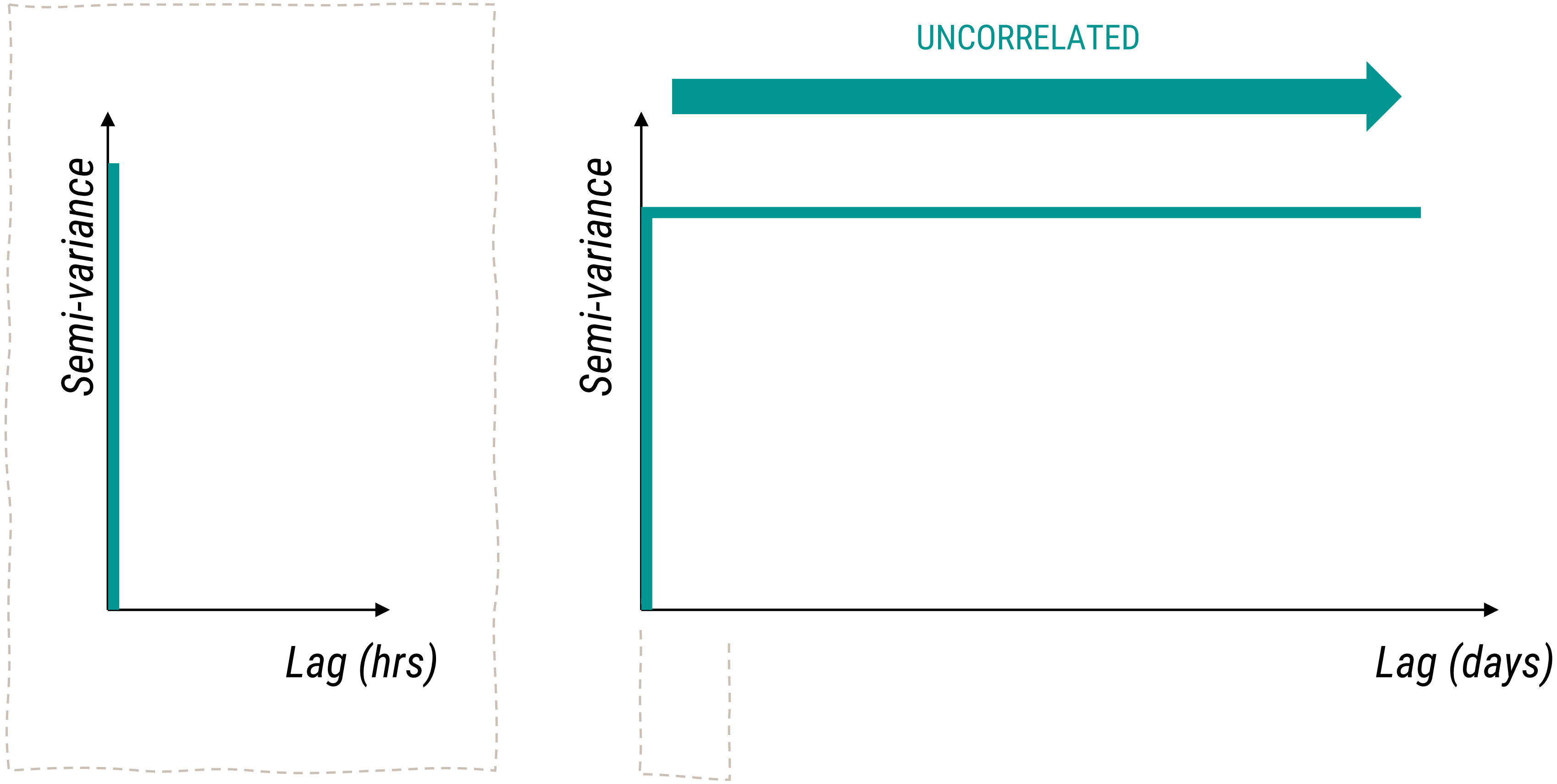
SPATIAL DEPENDENCY

TEMPORAL DEPENDENCY

RESTRICTED

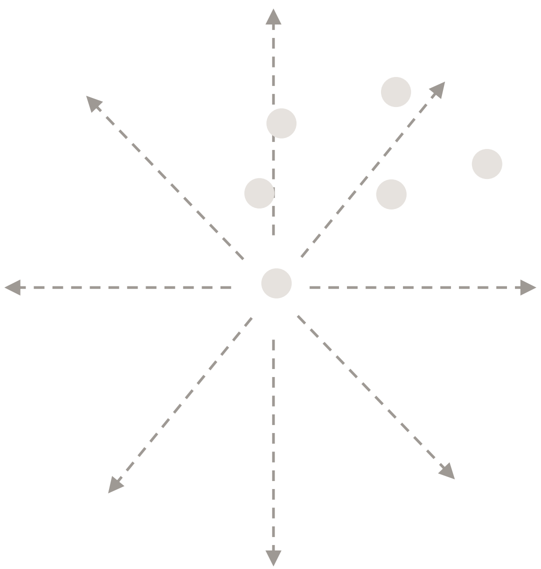
3.1. Independent and Identically Distributed (IID)

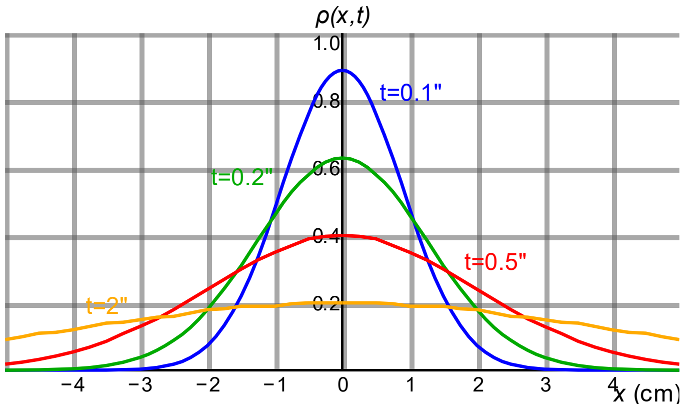
- How would the variogram of a IID process look like?



3.2. Brownian Motion (BM)

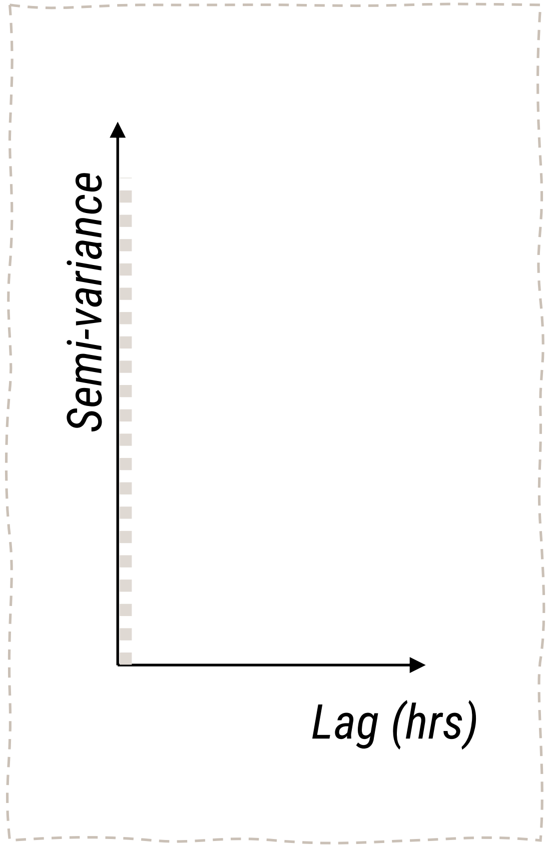
Stochastic process with stationary and independent increments, *i.e.*, no "memory" — the future behavior of a Brownian motion process does not depend on its past. Diffusion is constant.

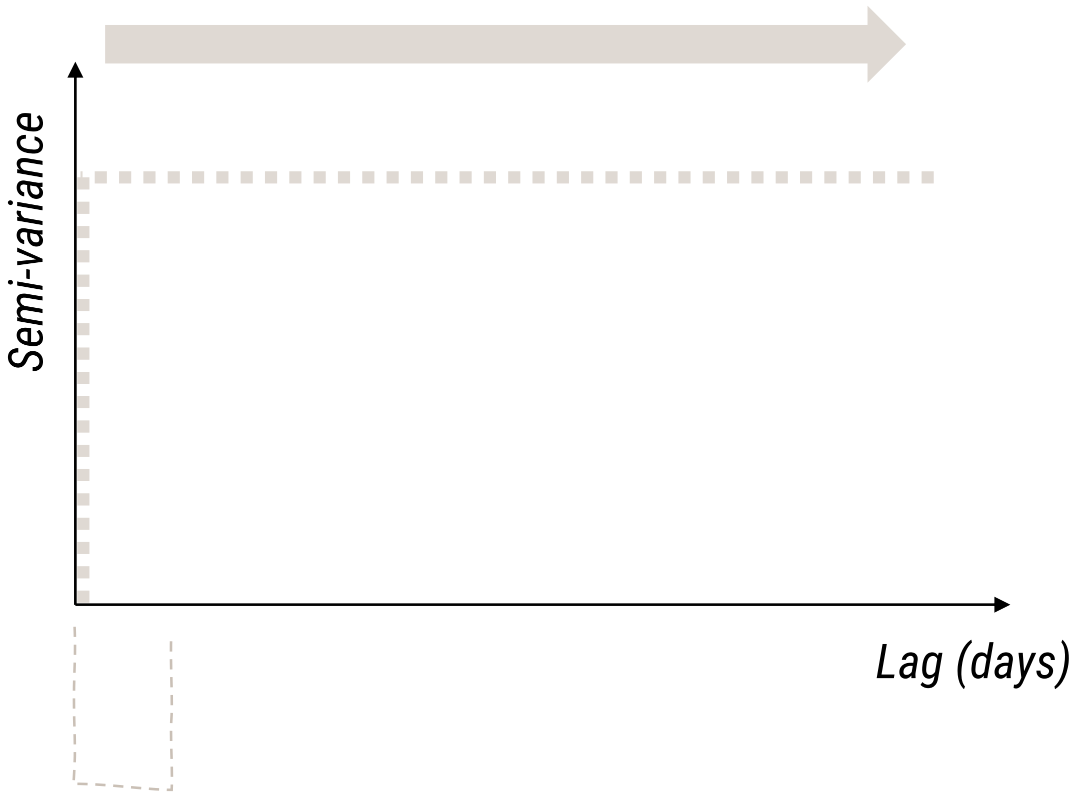




As time goes on, the animal is more likely to be further away from its starting location.

3.2. Brownian Motion (BM)





SPATIAL DEPENDENCY

TEMPORAL DEPENDENCY

RESTRICTED

3.2. Brownian Motion (BM)

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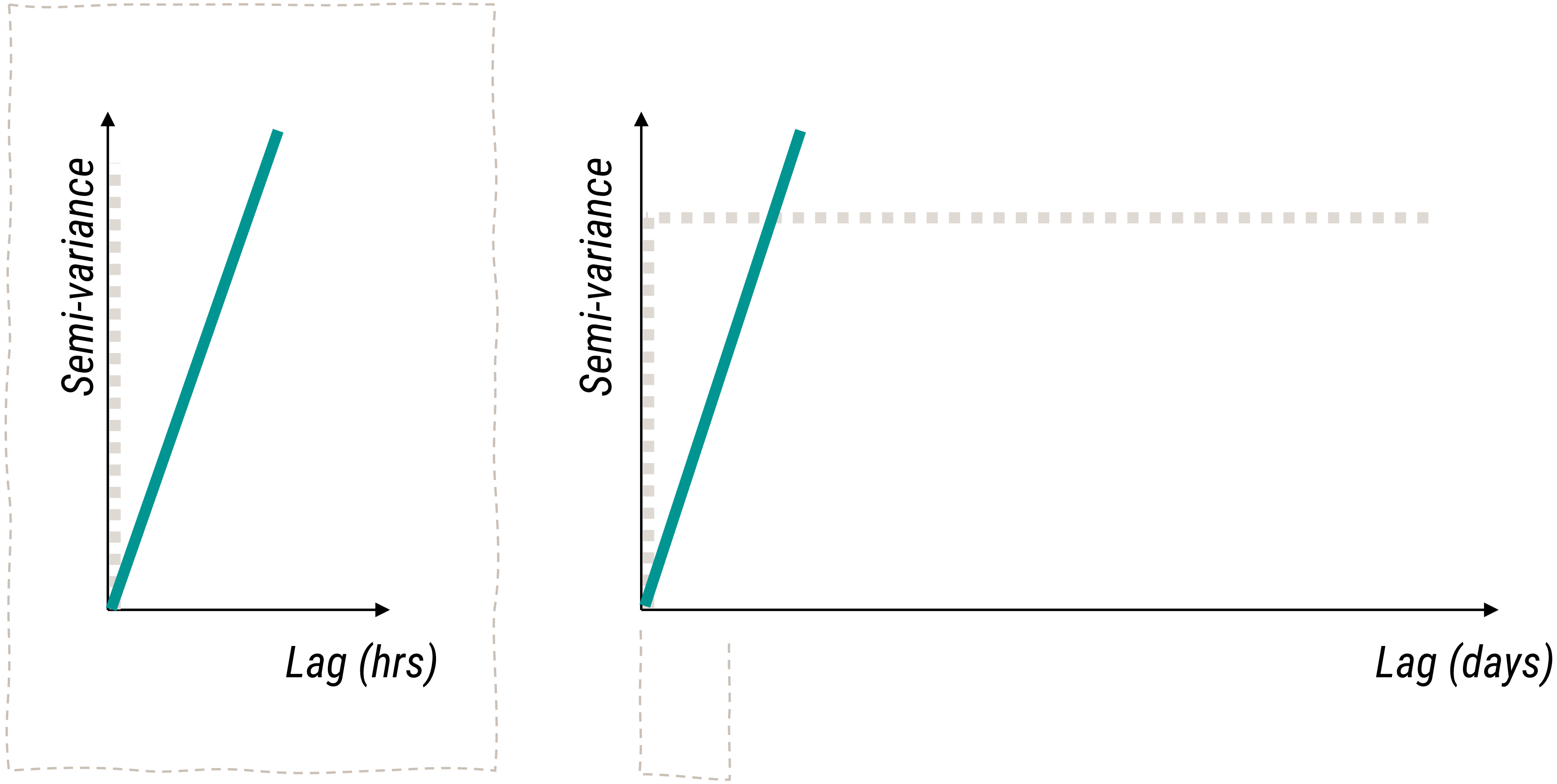
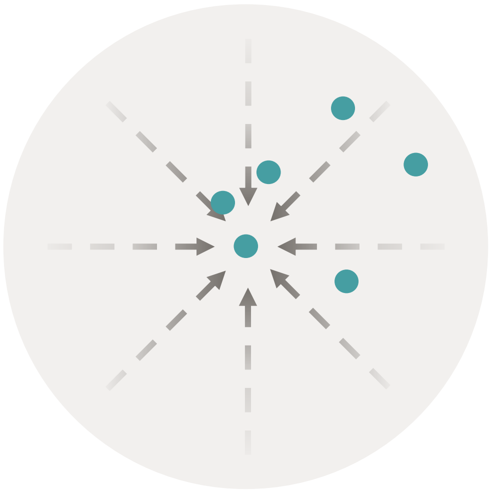


SPATIAL DEPENDENCY
TEMPORAL DEPENDENCY
RESTRICTED

These processes are all modifications of Brownian motion:

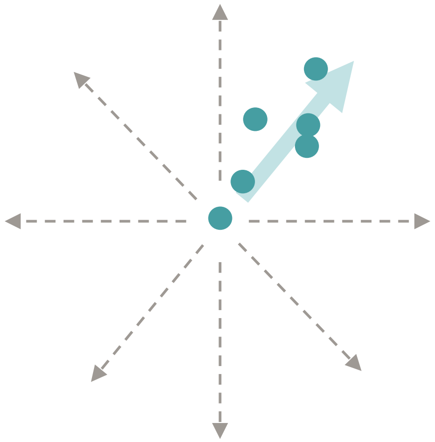
3.3. Ornstein-Uhlenbeck (OU)

- Unlike Brownian motion, OU tends to move back towards a central location (bounded), with a greater attraction the further away from the center.



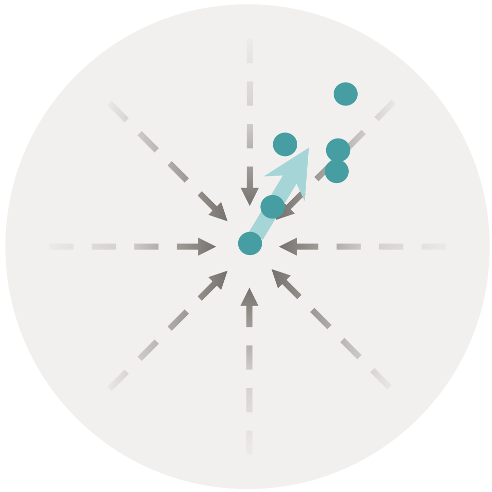
3.4. Integrated OU (IOU)

- Like Brownian motion, the integrated OU process exhibits unbounded diffusion, but with persistence of motion.



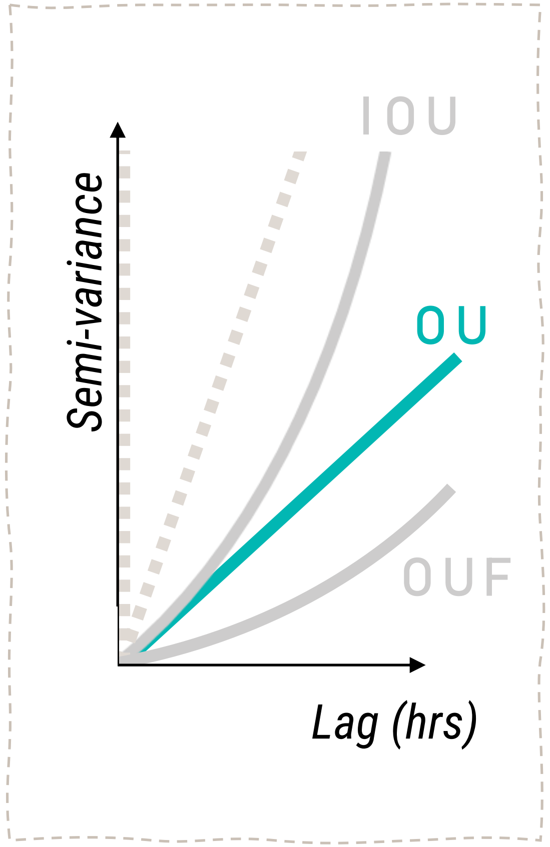
3.5. OU with Foraging (OUF)

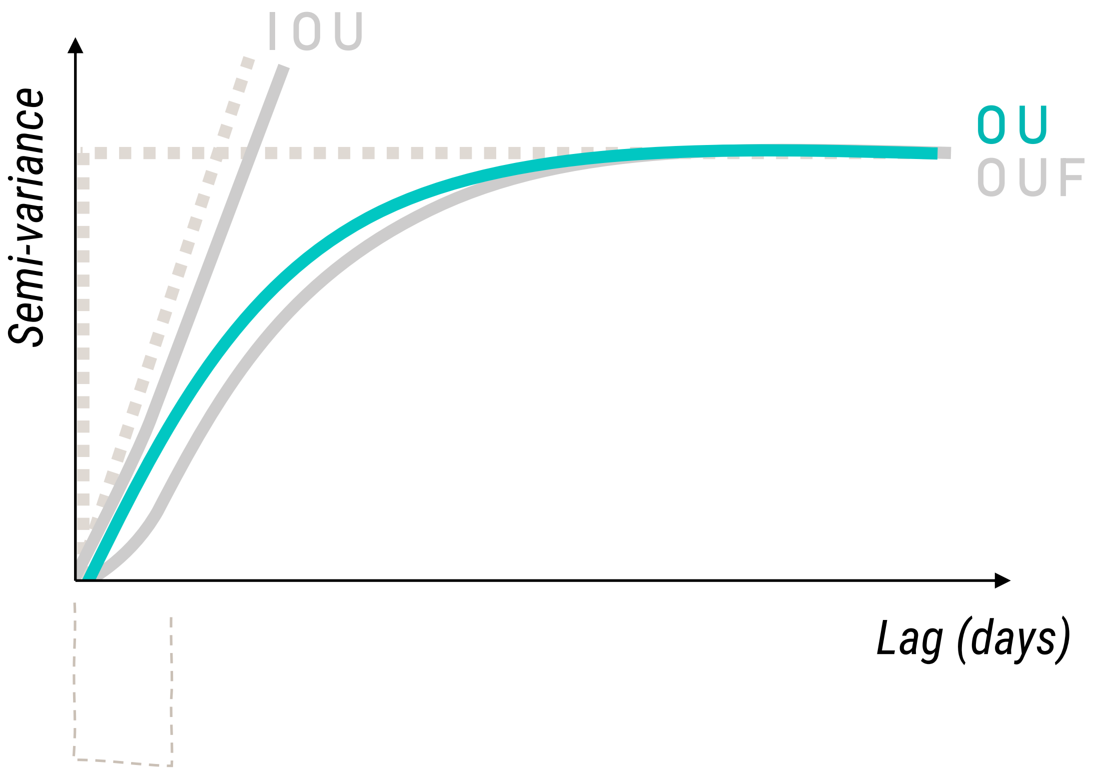
- Unlike Brownian motion, OUF is bounded, but with persistence of motion.



3.3. Ornstein-Uhlenbeck (OU)　　3.4. Integrated OU (IOU)　　3.5. OU with Foraging (OUF)

- How would the variograms of OU processes look like?





SPATIAL DEPENDENCY
TEMPORAL DEPENDENCY
RESTRICTED

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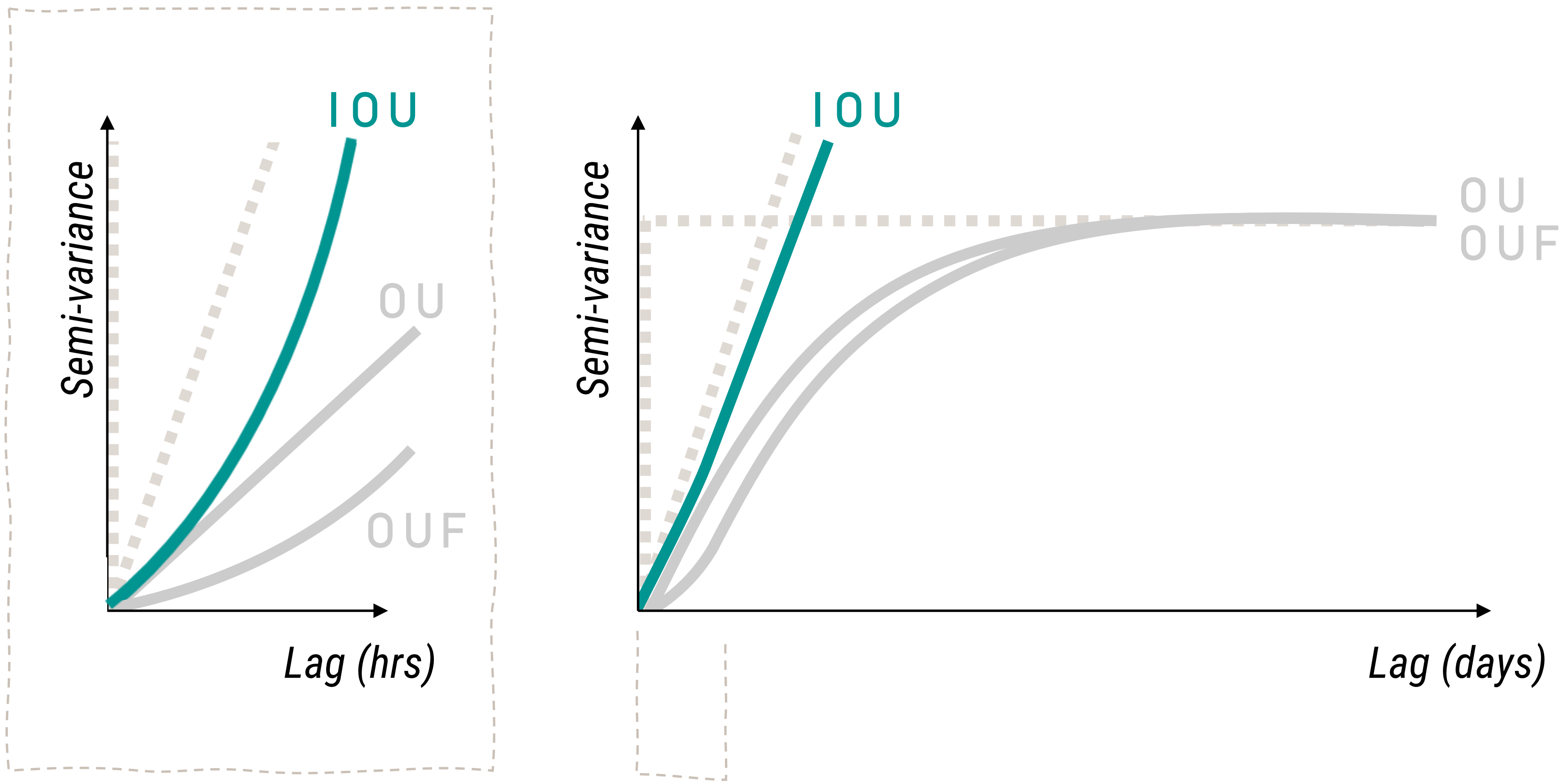

SPATIAL DEPENDENCY

TEMPORAL DEPENDENCY

RESTRICTED

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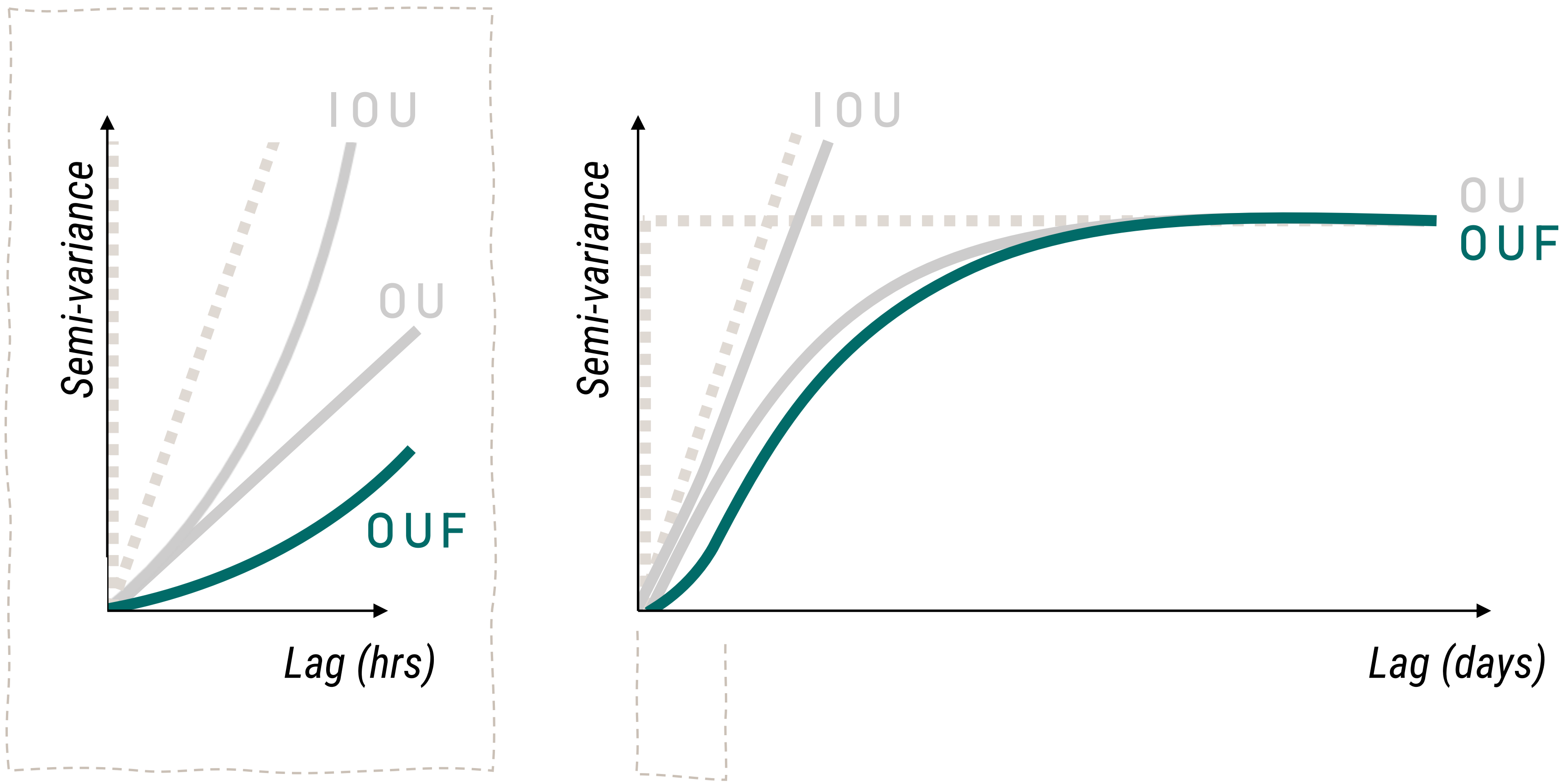
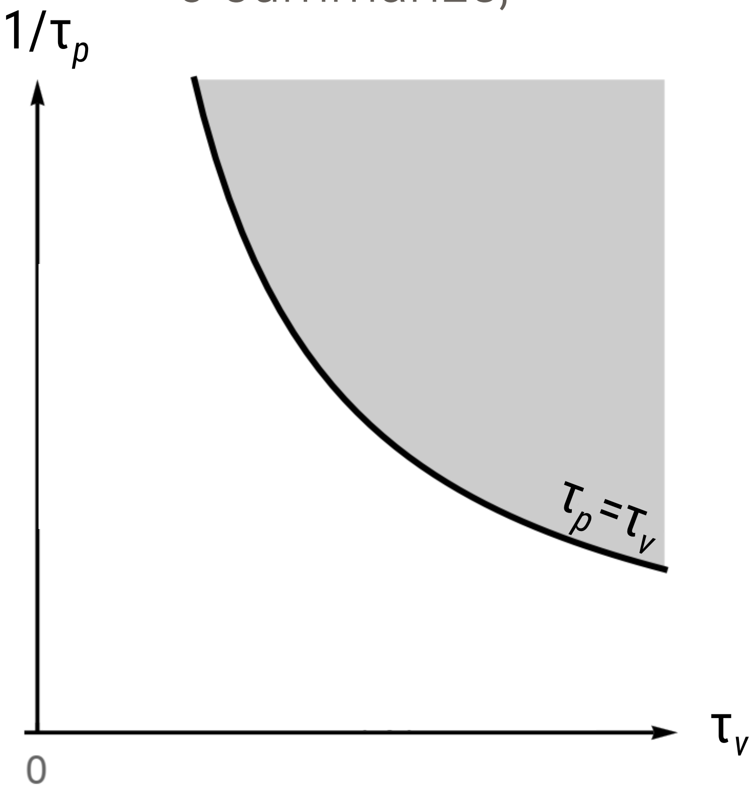


SPATIAL DEPENDENCY
TEMPORAL DEPENDENCY
RESTRICTED

To summarize,



	Autocorrelation			
Model	Position	Velocity	Restricted	Parameters:
IID	No	No	Yes	τ = NULL
BM	Yes	No	No	$\tau = \infty$
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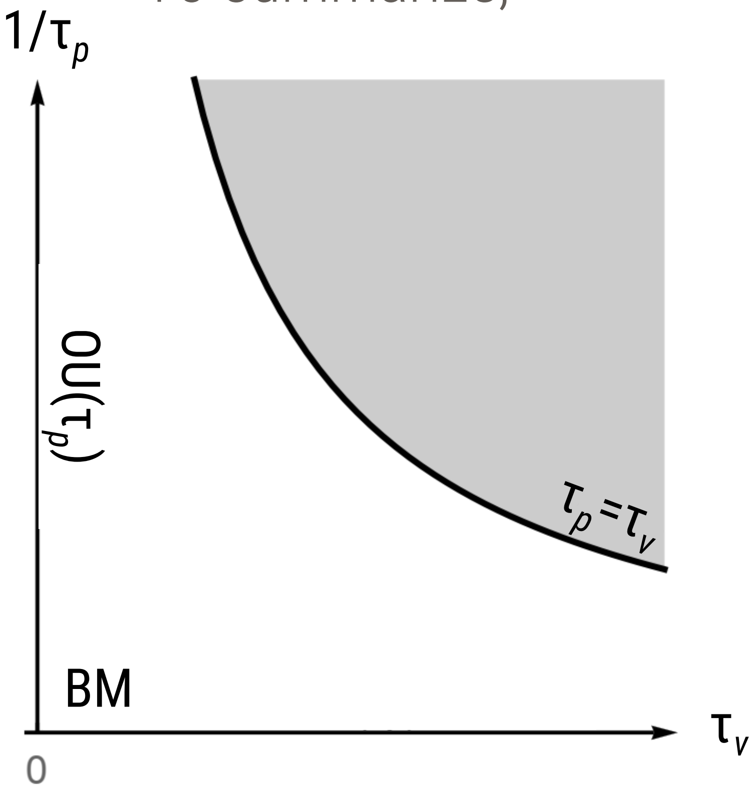

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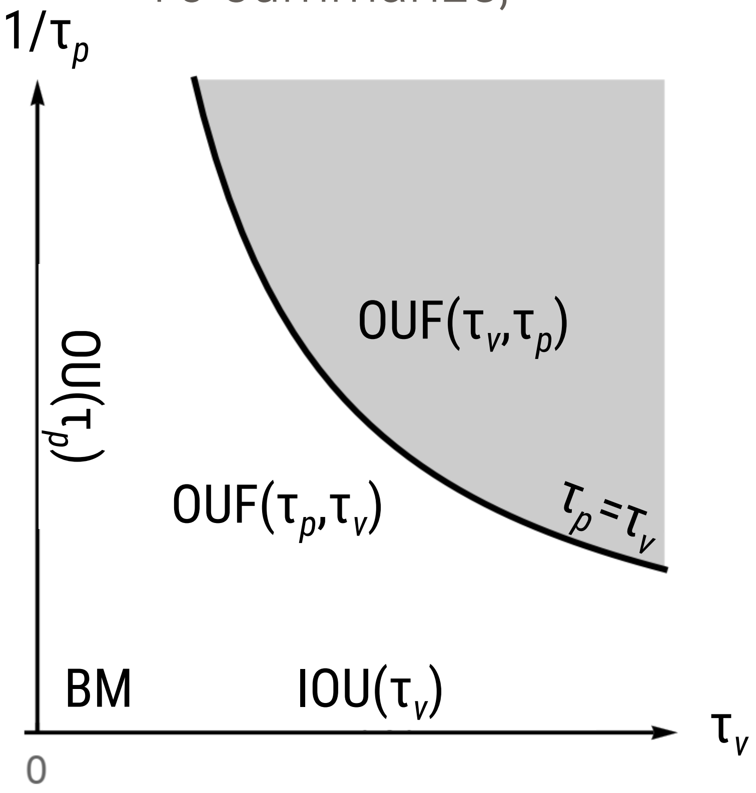

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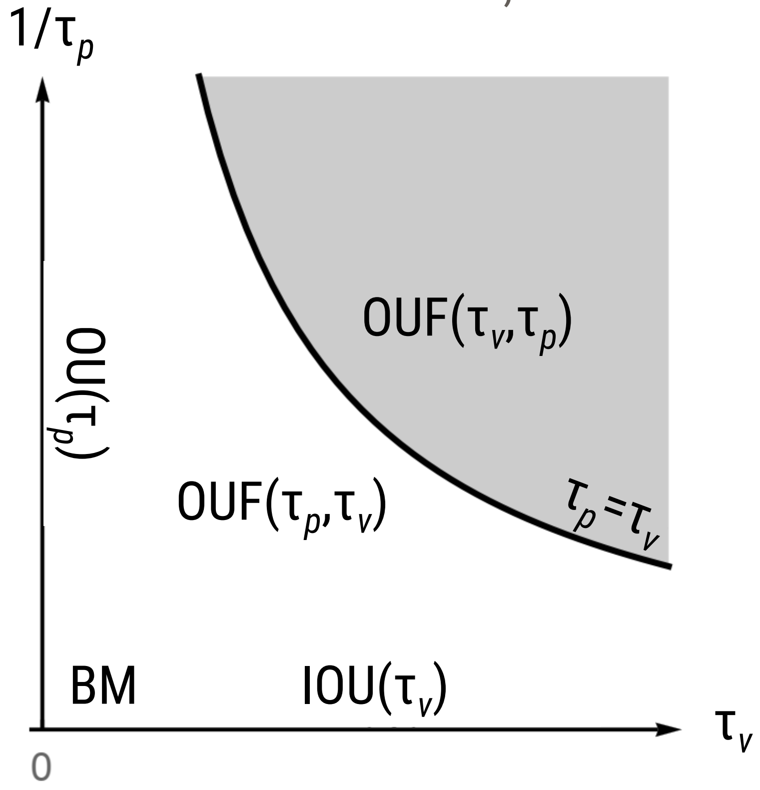
OU model itself still requires tracking data that are coarse enough to not show autocorrelated velocities, and many modern, high-resolution tracking datasets do not meet this criterion.

To summarize,



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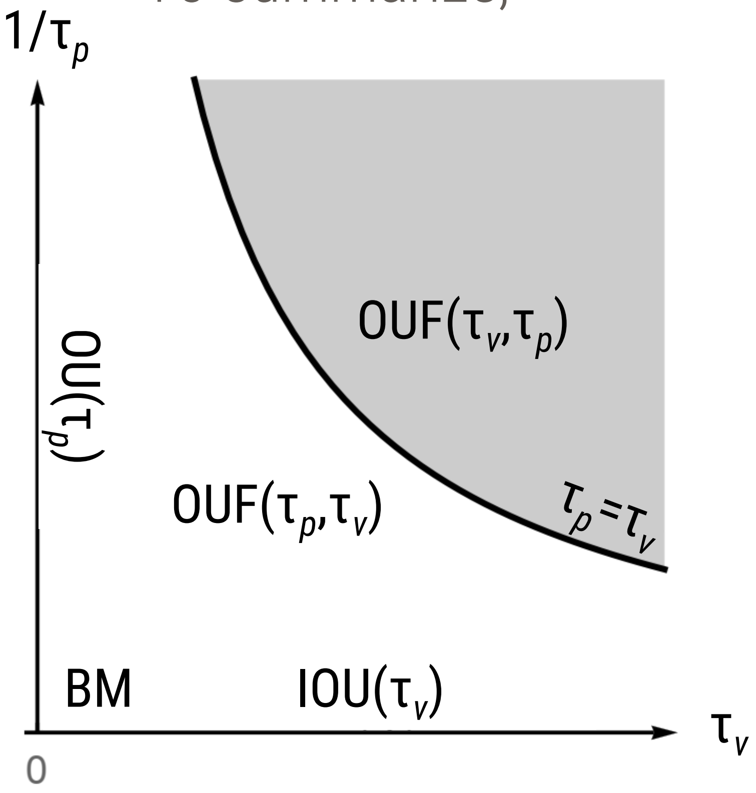

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> “All models are wrong, but some are useful.”
>
> Box *et al.* (1987)

Animal tracking data → **Fit movement model** → Estimate home range

What movement model parameters are most likely to characterize a given tracking dataset?

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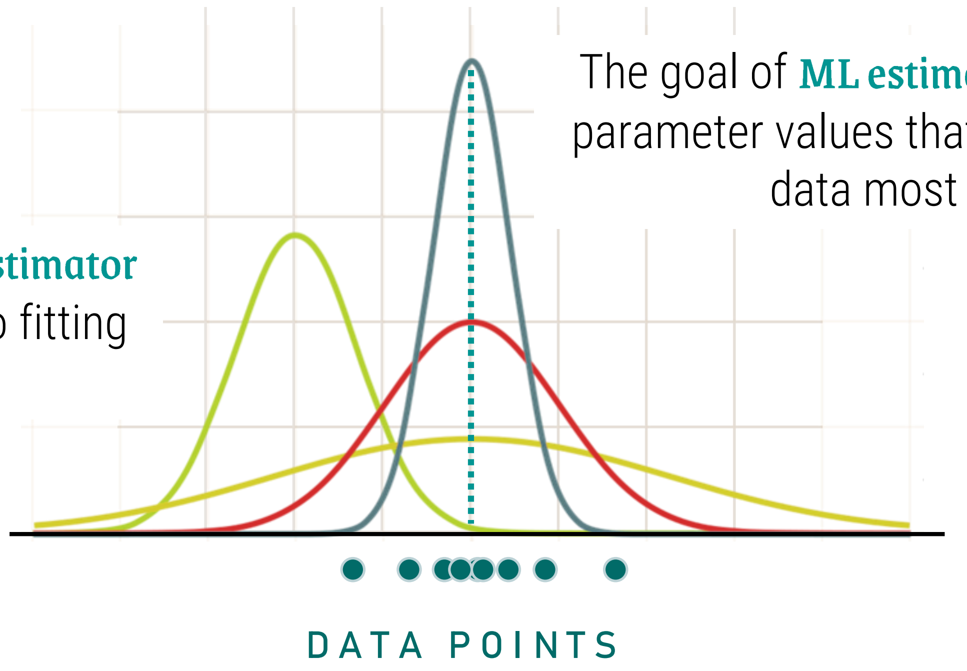
$$\underbrace{\tau_p \qquad \tau_v}_{\text{One or more (unknown) parameters}}$$

Animal tracking data → Fit movement model → Estimate home range

What movement model parameters are most likely to characterize a given tracking dataset?

MAXIMUM LIKELIHOOD:

Maximum Likelihood (ML) estimator is the standard approach to fitting movement models.



The goal of **ML estimation** is to select the parameter values that make the observed data most probable.

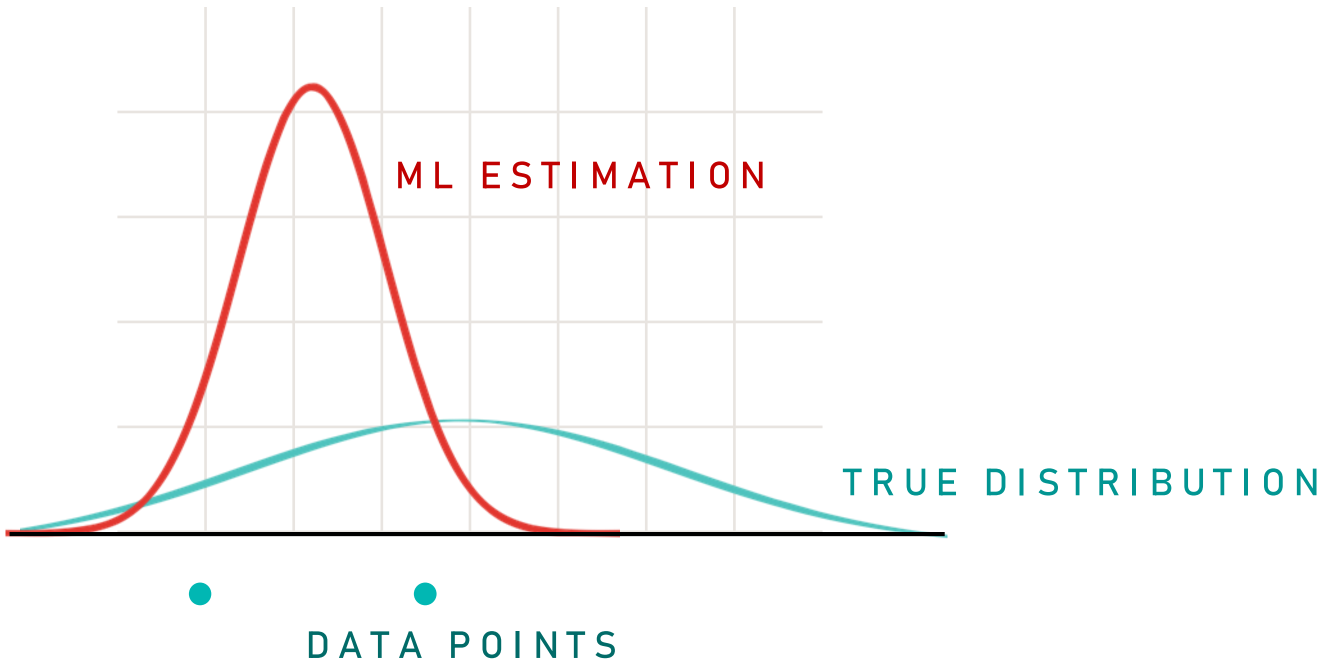
Animal tracking data → Fit movement model → Estimate home range

What movement model parameters are most likely to characterize a given tracking dataset?

MAXIMUM LIKELIHOOD:

Unfortunately, **ML** performs poorly at small sample sizes

(Cressie, 1993)



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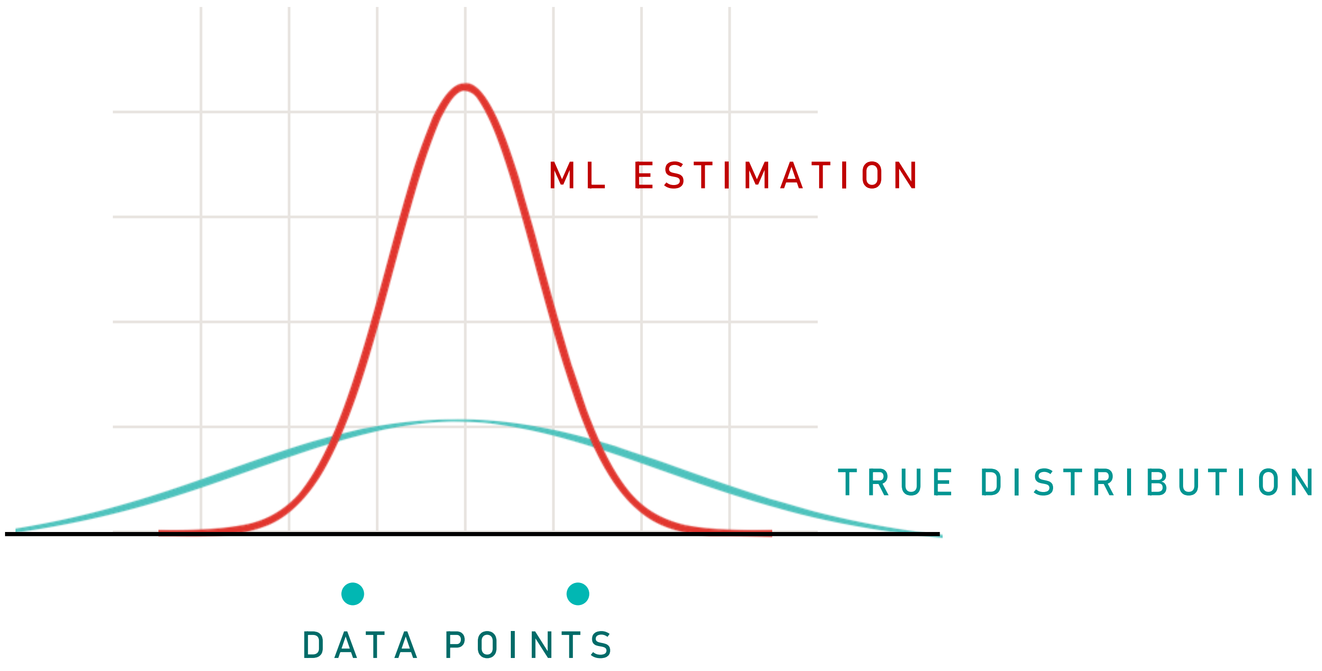

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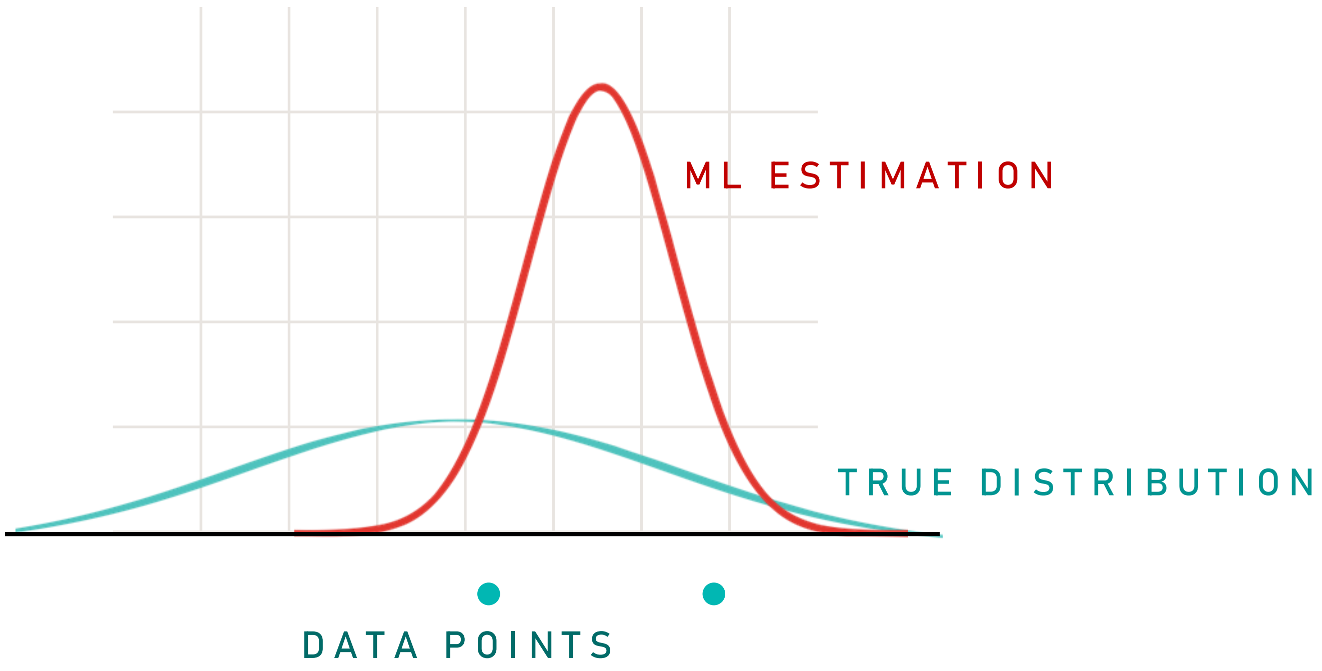

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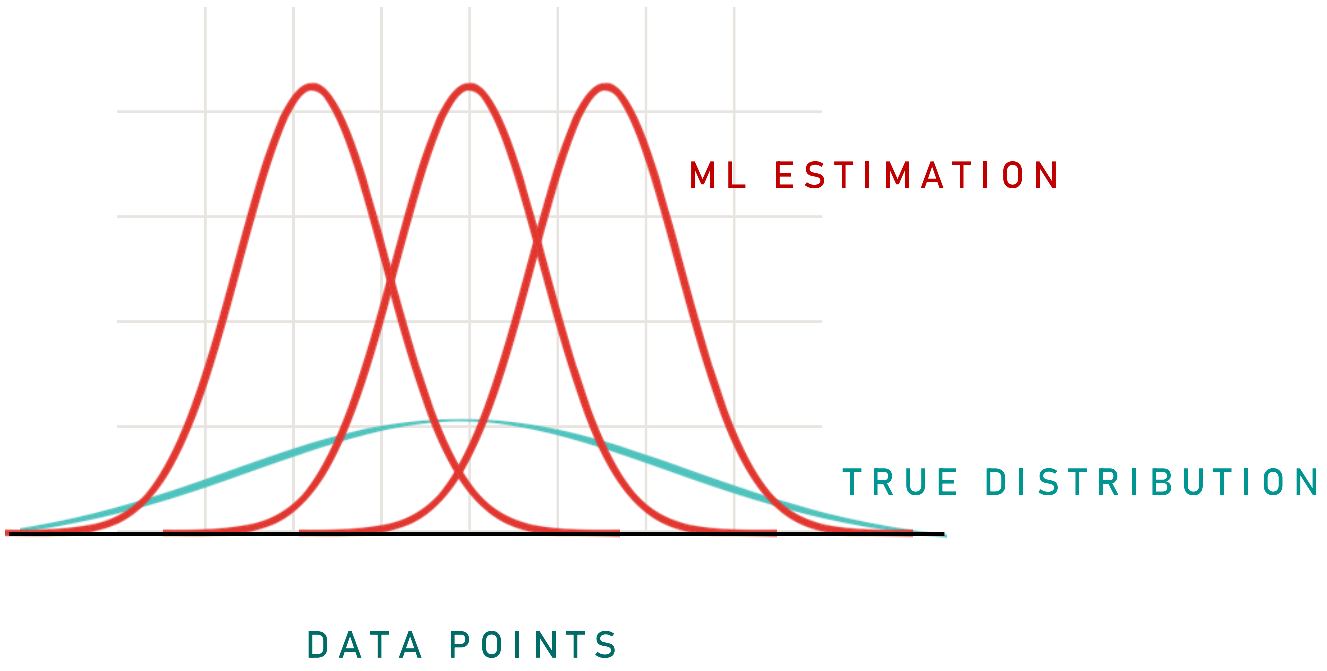


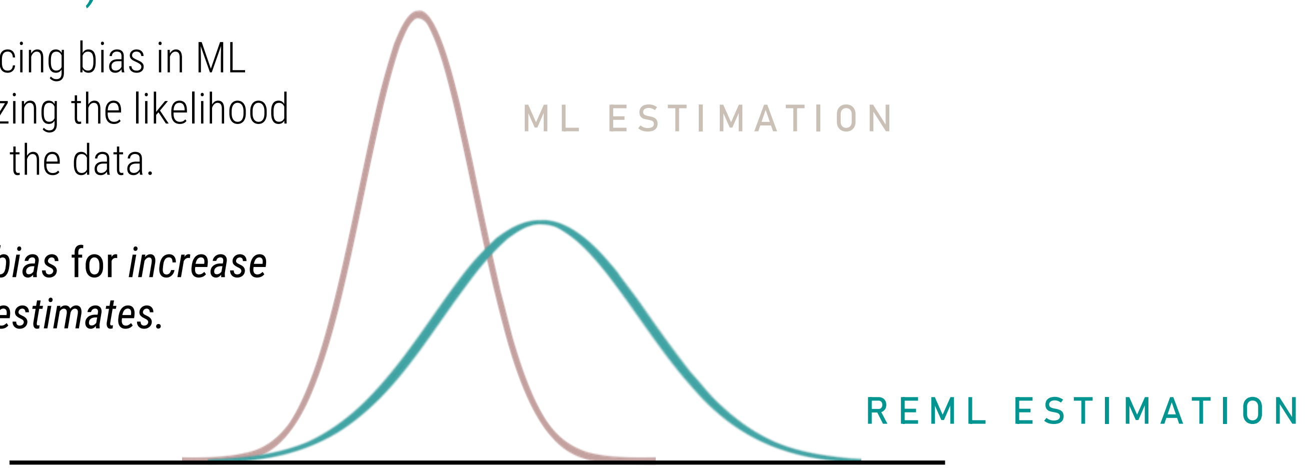
We can tackle the ML bias in several ways.
For example:

Residual ML (or REML)

Widely used method for reducing bias in ML variance estimation, by maximizing the likelihood of residuals rather than the data.

Essentially, it trades *reduced bias* for *increase variability in parameter estimates.*

(Bartlett, 1937)



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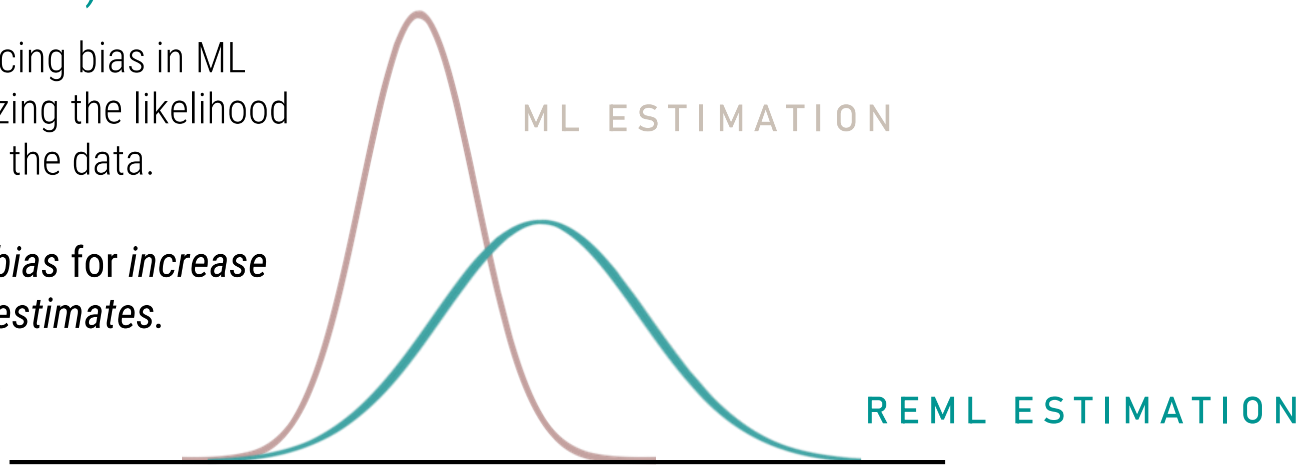

However, REML is not always ideal for animal tracking data.

WORKFLOW:

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Checking if data is from a range-resident animal

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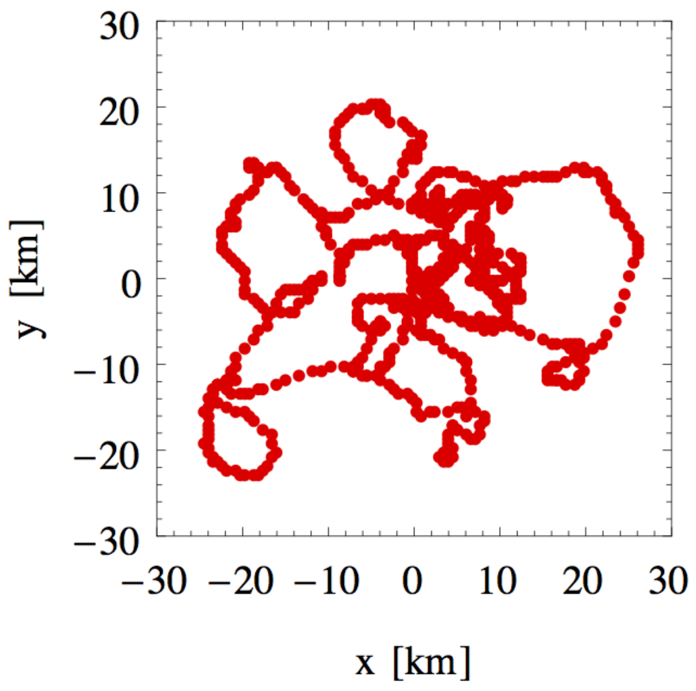
Tracking data → Fit movement model → Estimate home range

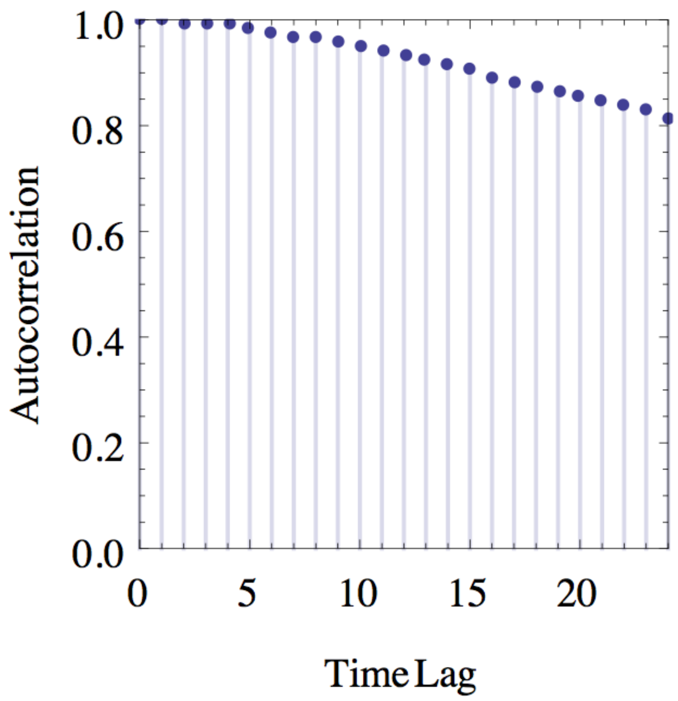
Autocorrelated Kernel Density Estimator (AKDE)

Described in Fleming *et al.* (2015)

DOI: 10.1890/14-2010.1

As sampling frequency increases, so does the autocorrelation.





HR ESTIMATION

Tracking data → Fit movement model → Estimate home range

Autocorrelated Kernel Density Estimator (AKDE)

Described in Fleming *et al.* (2015)

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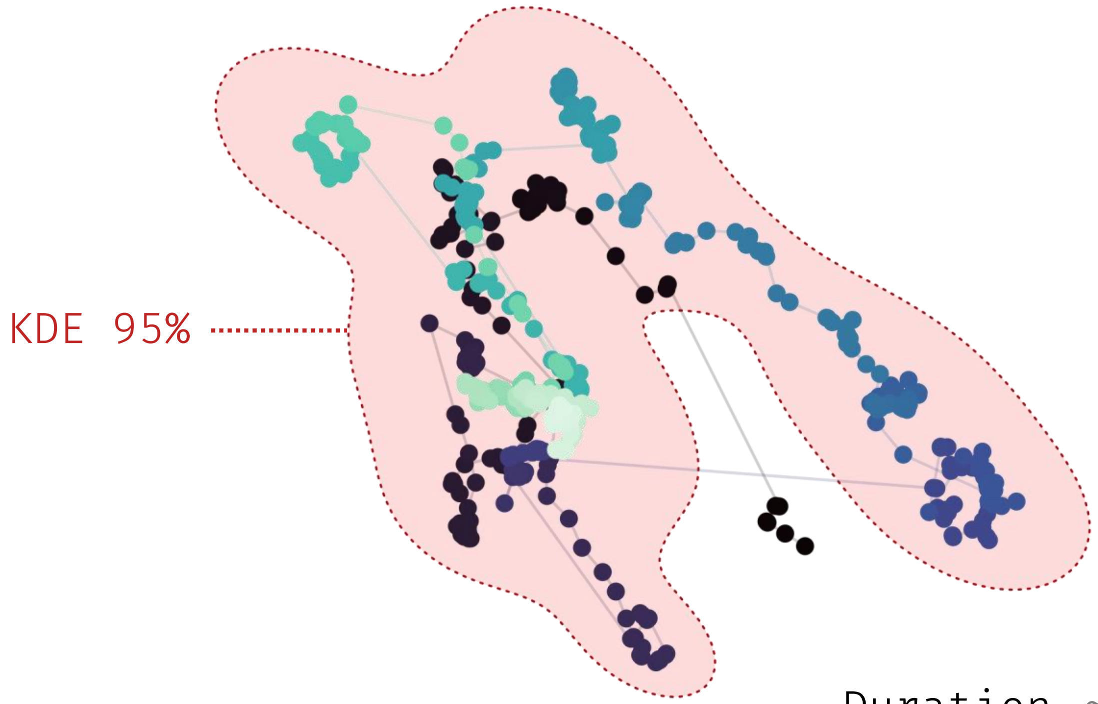
Re-derived KDE that explicitly assumes the data represents a sample from a **nonstationary, autocorrelated, continuous movement process**.



Duration ≈ 1 year
τ_p ≈ 2.4 months

Tracking data → Fit movement model → Estimate home range

Autocorrelated Kernel Density Estimator (AKDE)

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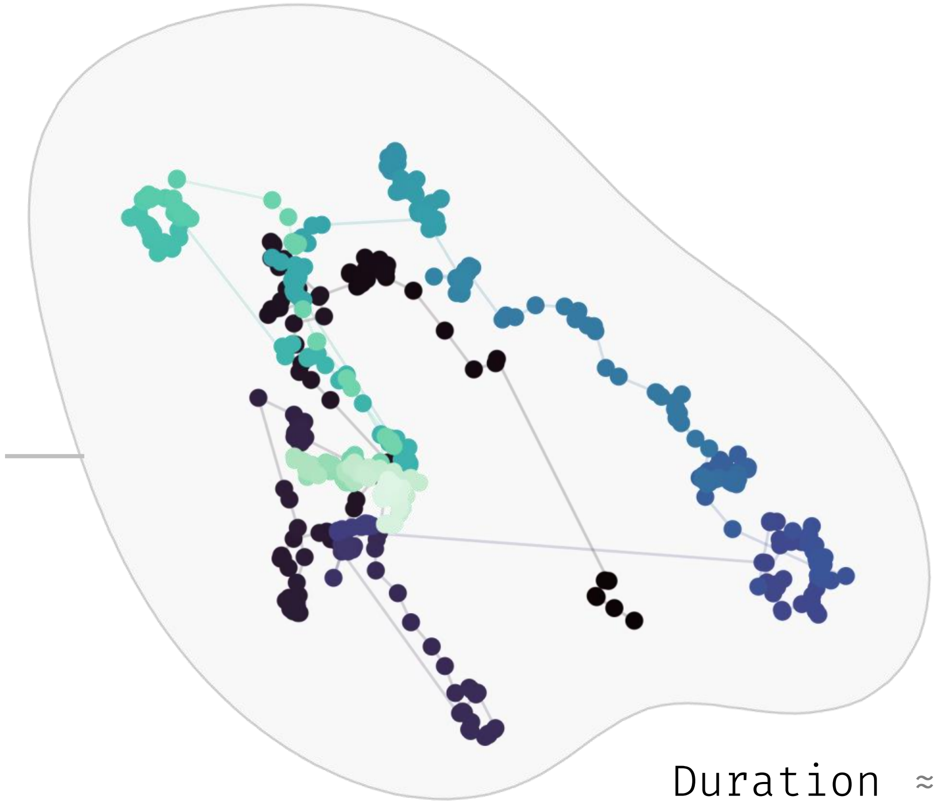
DOI: 10.1890/14-2010.1

AKDE 95%



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Tracking data → Fit movement model → Estimate home range

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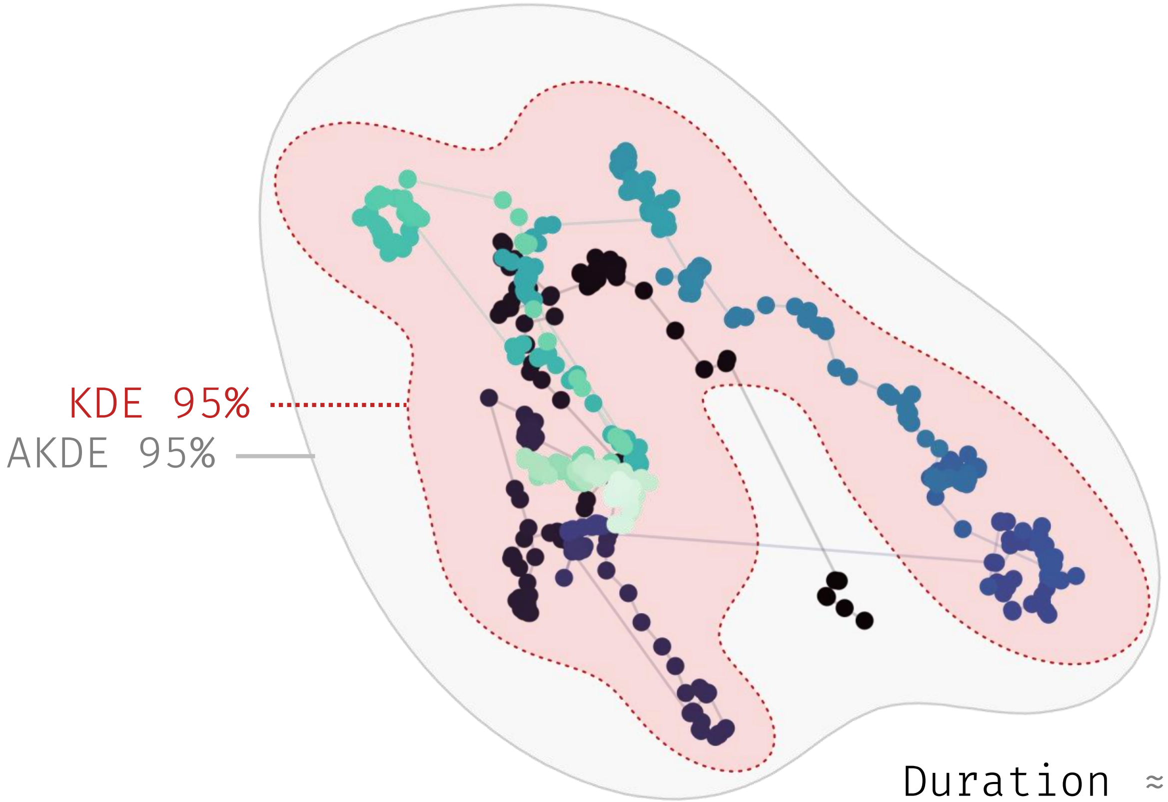

Re-derived KDE that explicitly assumes the data represents a sample from a **nonstationary, autocorrelated, continuous movement process**.

Duration ≈ 1 year
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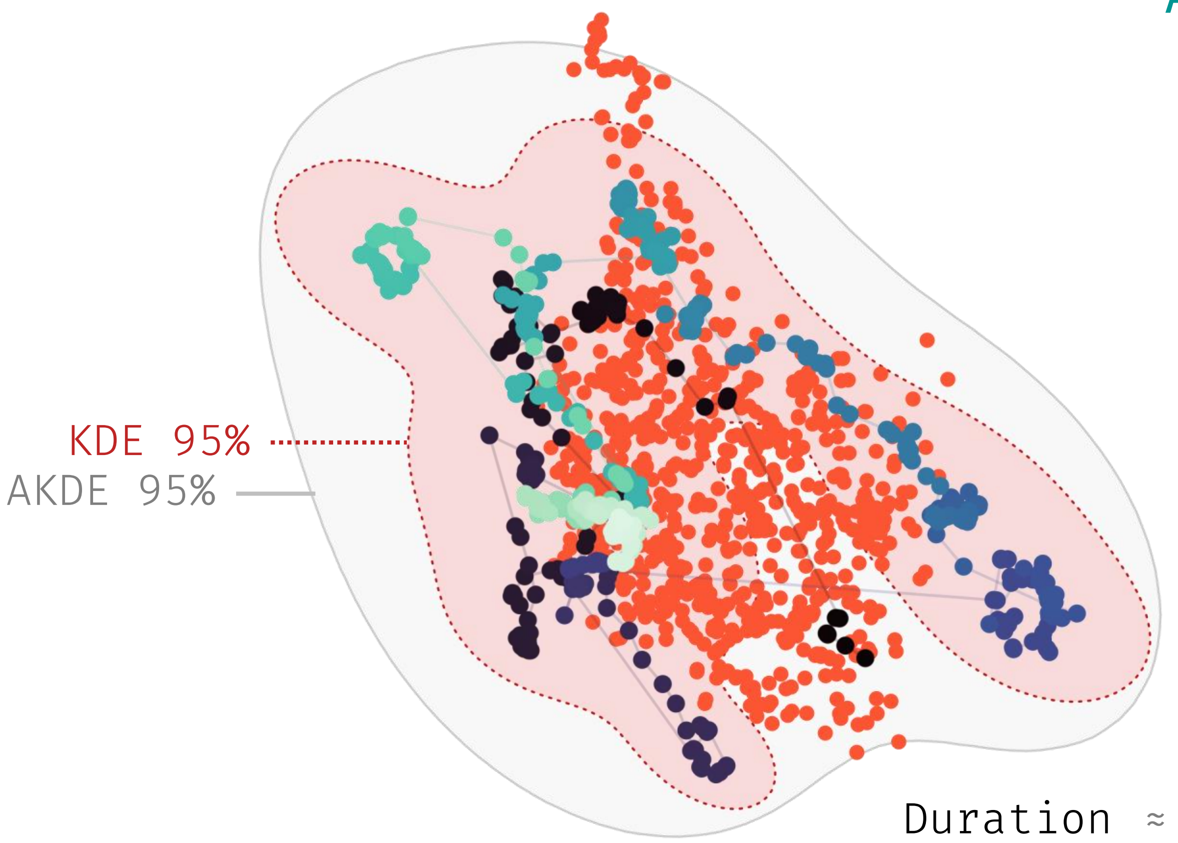
HR ESTIMATION

Tracking data → Fit movement model → **Estimate home range**



Autocorrelated Kernel Density Estimator (AKDE)

Described in Fleming *et al.* (2015)

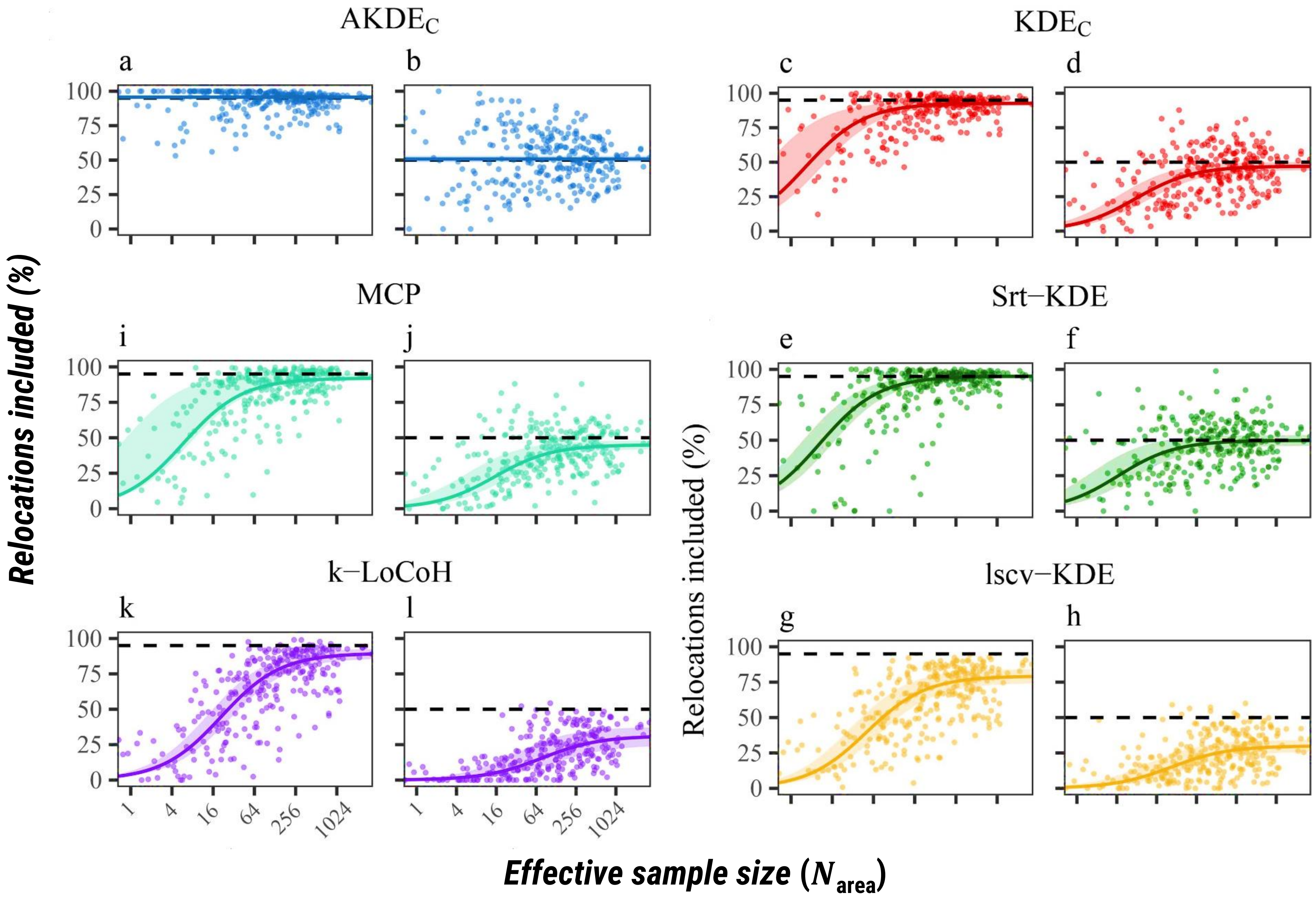
DOI: 10.1890/14-2010.1

Re-derived KDE that explicitly assumes the data represents a sample from a **nonstationary, autocorrelated, continuous movement process**.

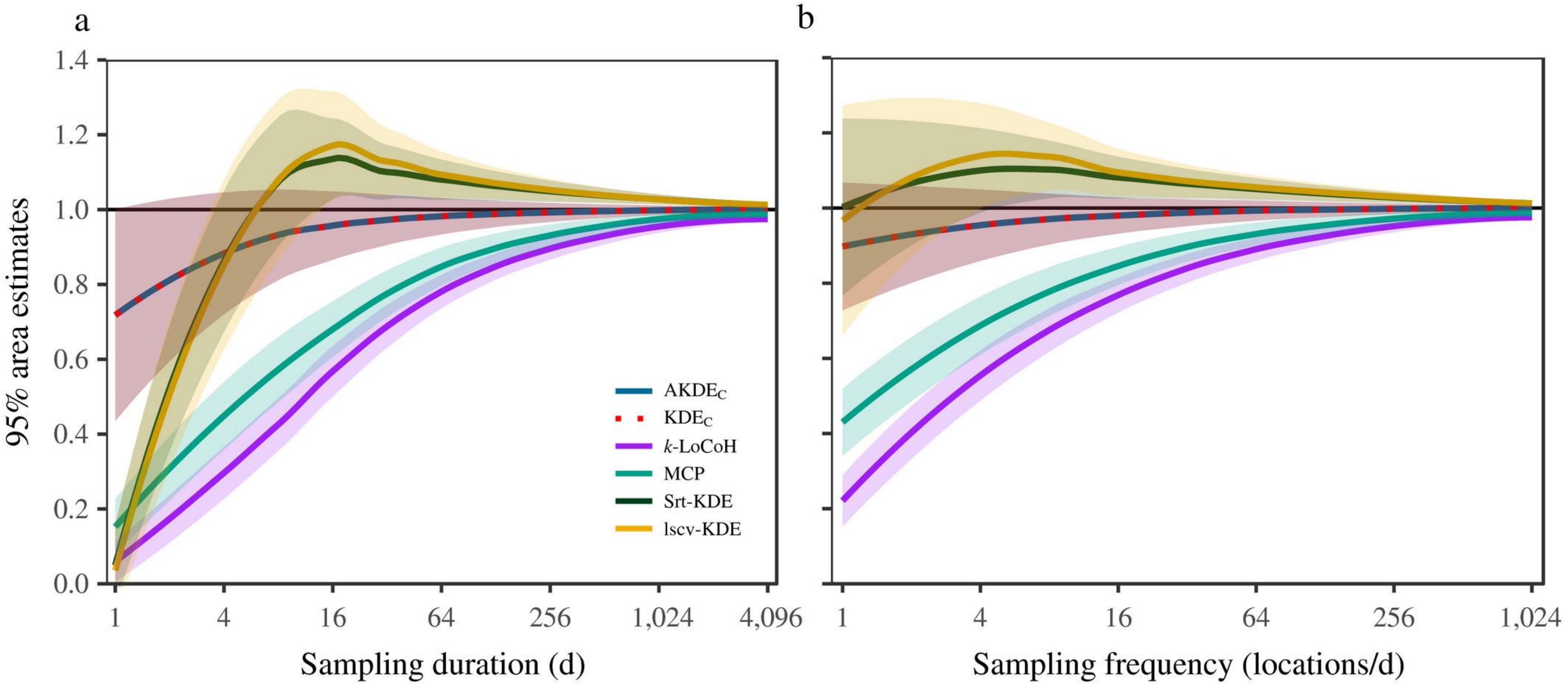
Duration ≈ 1 year → Extrapolated to 2 years

τ_p ≈ 2.4 months

STEP 3



AKDE$_C$
KDE$_C$
MCP
Srt−KDE
k−LoCoH
lscv−KDE
a
b
c
d
e
f
g
h
i
j
k
l
100
75
50
25
0
1
4
16
64
256
1024
Relocations included (%)
Effective sample size (N_{area})



Conventional KDEc, and MCP estimates were, on average, smaller than AKDEc's estimates by a factor of ~ 3, and by a factor of ~ 13 for lscv-KDE and *k*-LoCoH.

Tracking data → Fit movement model → Estimate home range

	Autocorrelation			
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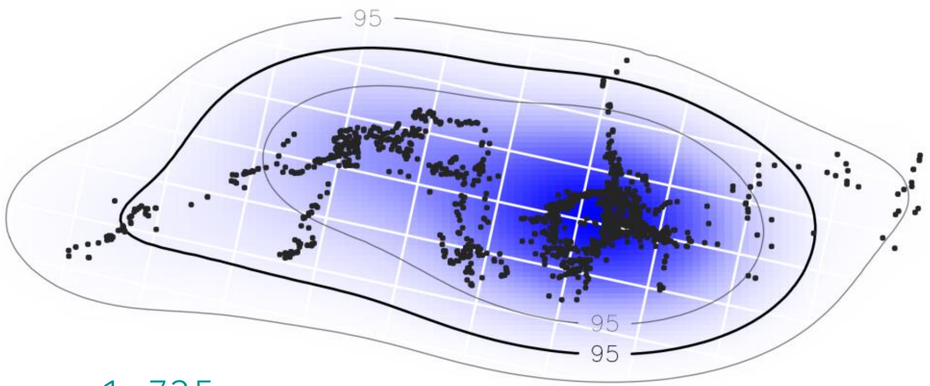
AKDEs explicitly requires a movement model that accounts *autocorrelated* data.

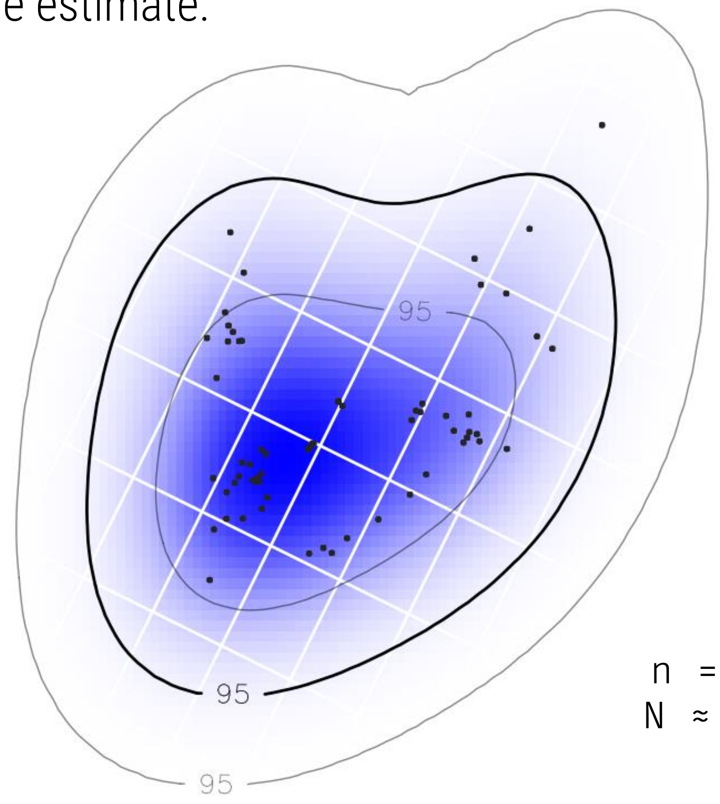
AKDE reduces to the conventional **KDE** in the limit where autocorrelation vanishes, and locations are truly independent.

AKDEs also provide accurate confidence intervals that can diagnose situations where the data are insufficient to provide a reasonable home range estimate.



n = 1,725
N ≈ 15.7

Area estimate
757.5 km² (430.0 – 1,176.2)

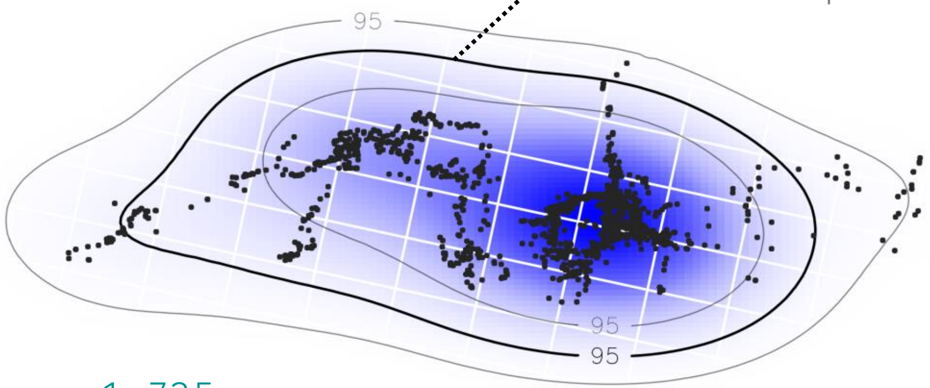


n = 66
N ≈ 6.9

Area estimate
4,232.3 km² (1,681.7 – 7,939.5)

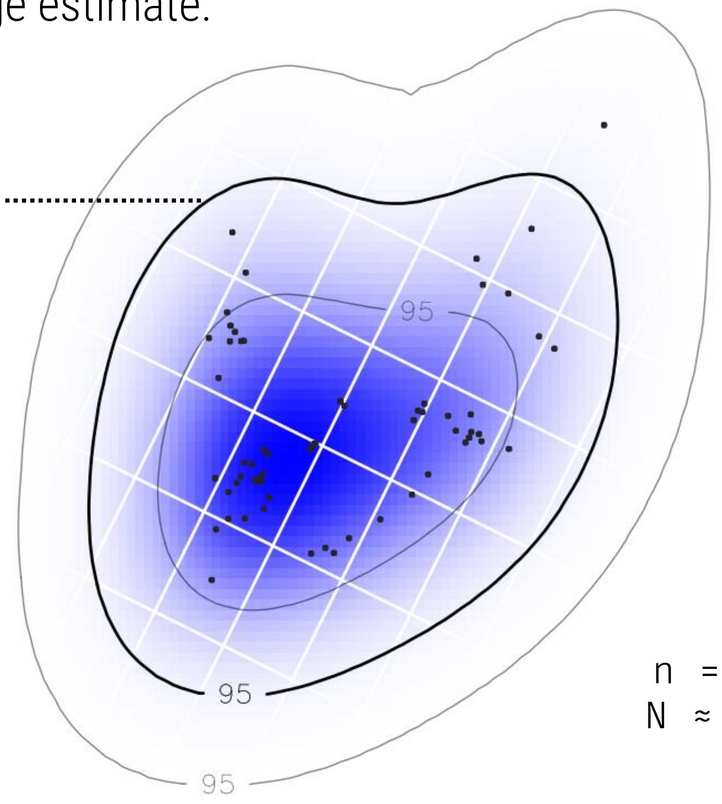
AKDEs also provide accurate confidence intervals that can diagnose situations where the data are insufficient to provide a reasonable home range estimate.

The 95% contour represents the maximum likelihood area where the animal spends 95% of its time.



n = 1,725
N ≈ 15.7

Area estimate
757.5 km² (430.0 – 1,176.2)



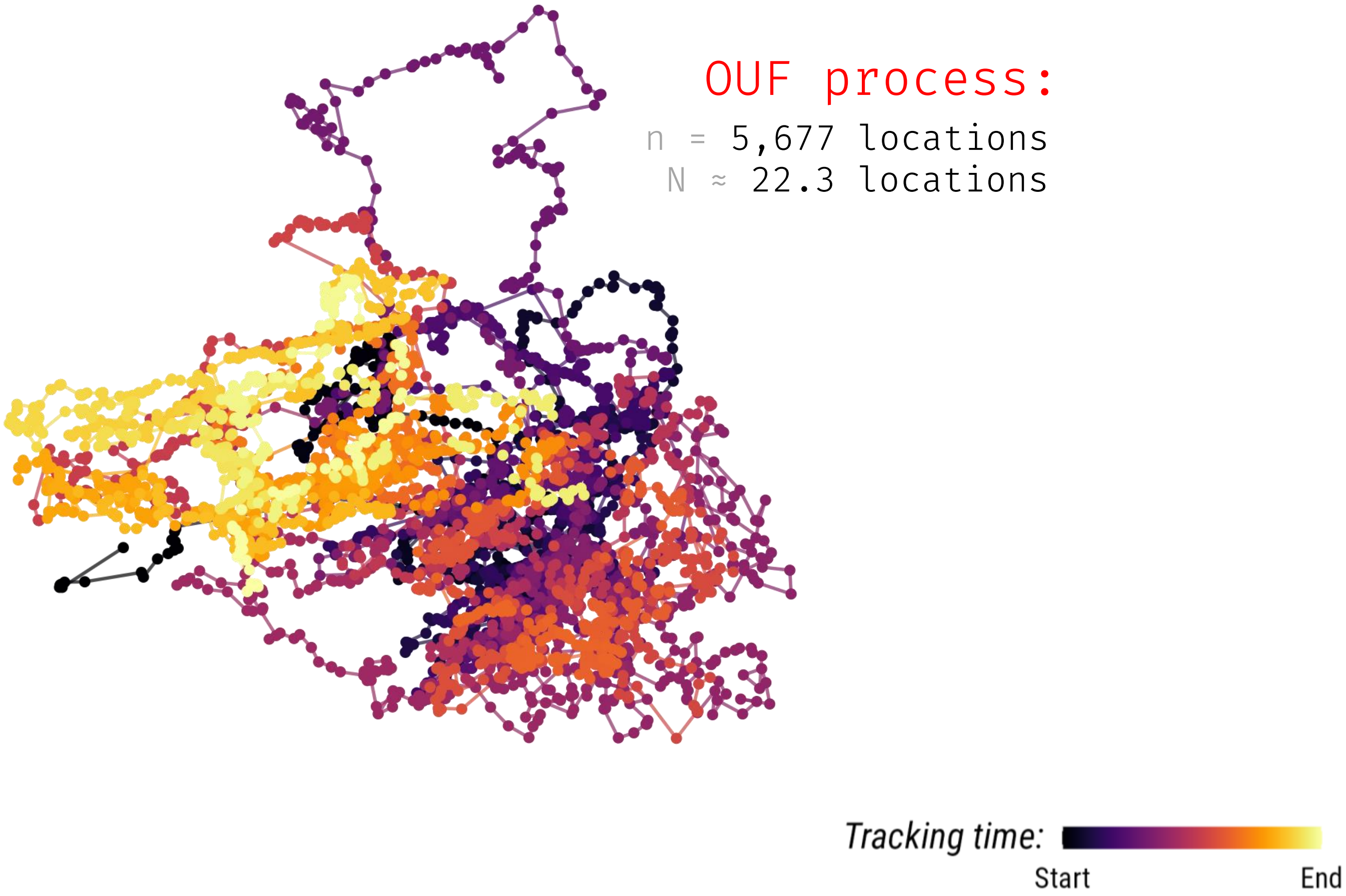
n = 66
N ≈ 6.9

Area estimate
4,232.3 km² (1,681.7 – 7,939.5)

HR ESTIMATION

AFRICAN BUFFALO

SYNCERUS CAFFER

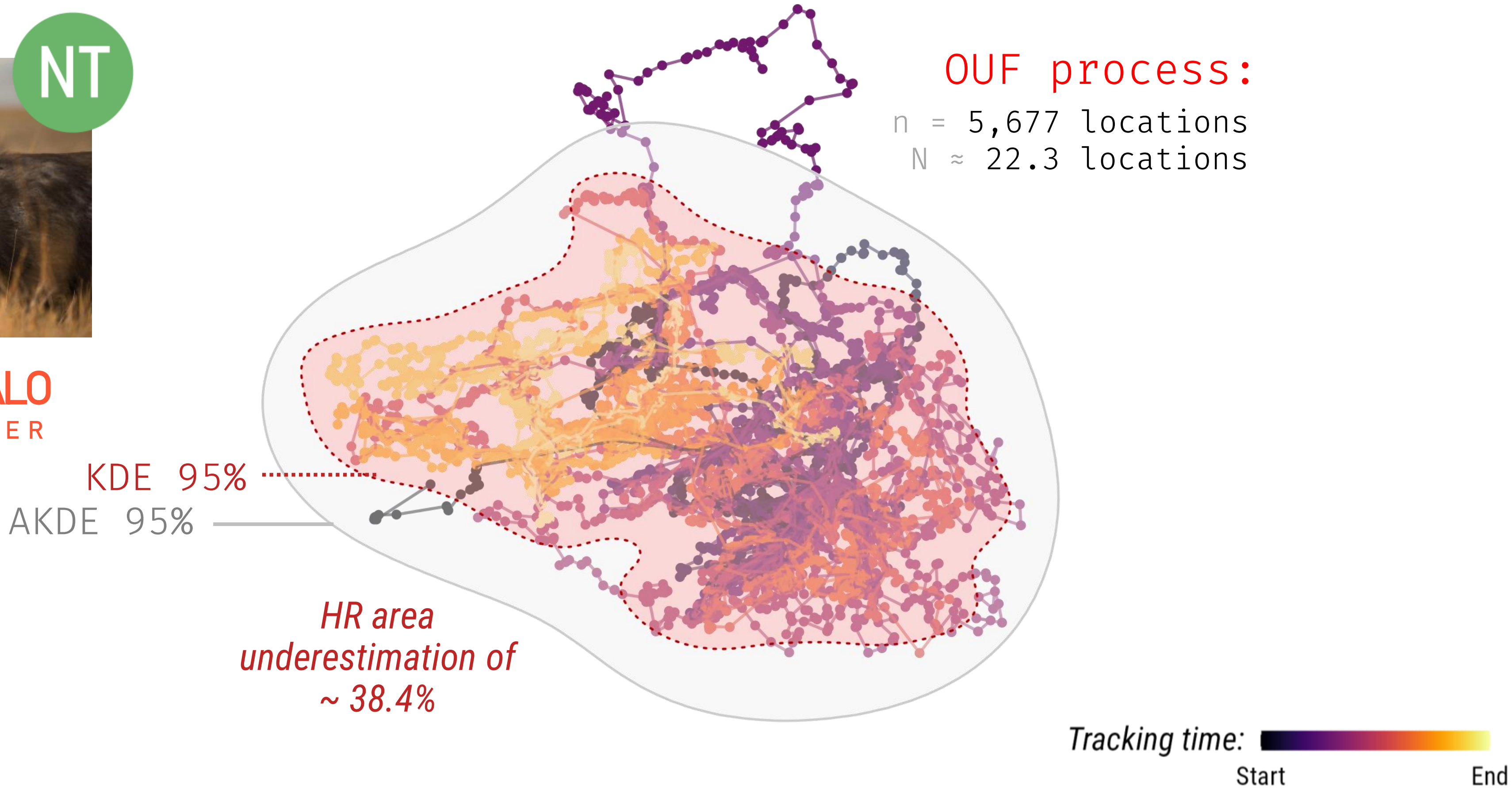


STEP 3

HR ESTIMATION

AFRICAN BUFFALO

SYNCERUS CAFFER

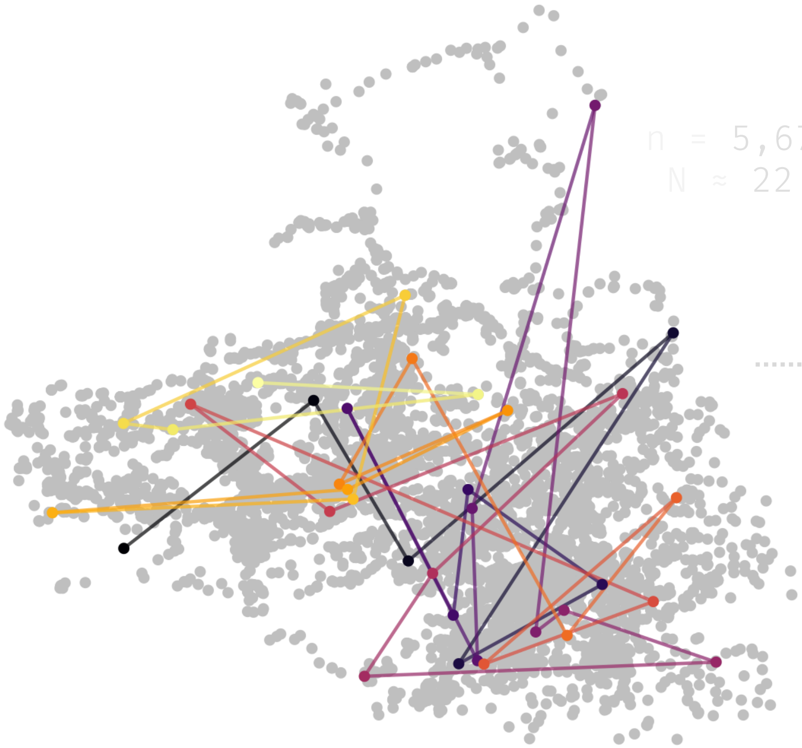


STEP 3

HR ESTIMATION

AFRICAN BUFFALO

SYNCERUS CAFFER



IID process:

n = 35 locations
N ≈ 35 locations

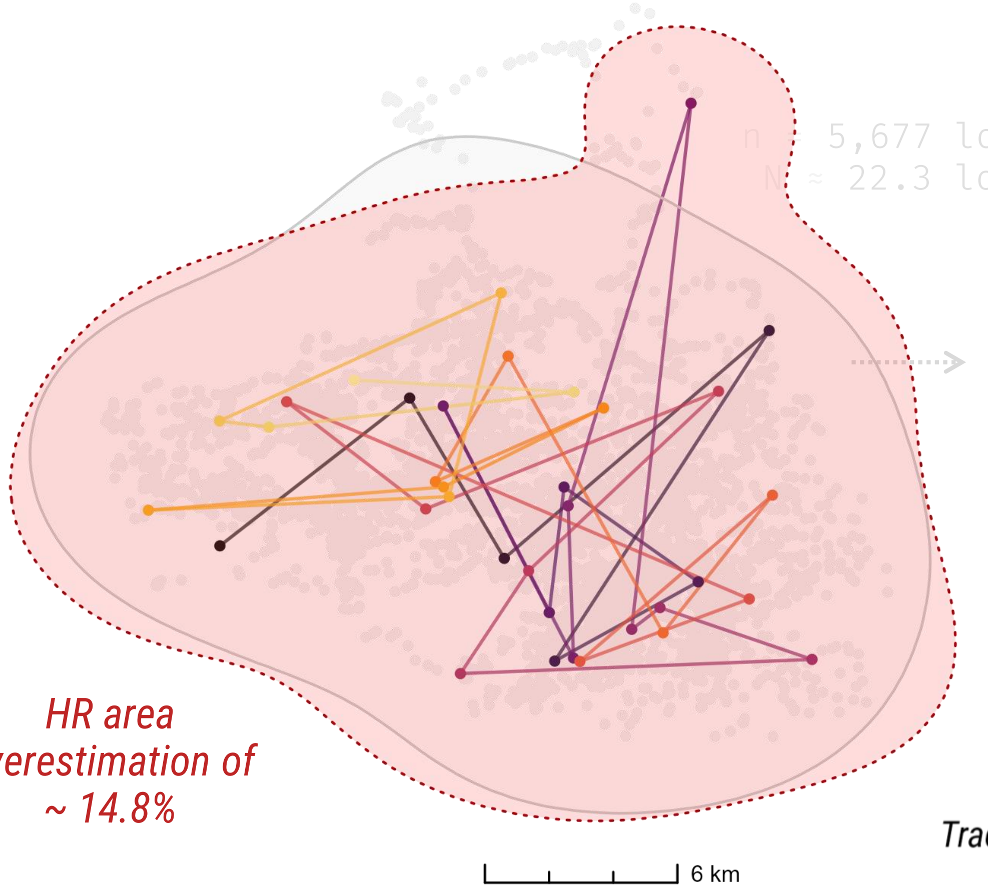
Data loss of ≈ 99.4%

Tracking time: Start End

HR ESTIMATION

AFRICAN BUFFALO

SYNCERUS CAFFER



IID process:

n = 35 locations

N ≈ 35 locations

Data loss of ≈ 99.4%

HR area overestimation of ~ 14.8%

Tracking time: Start End

WORKFLOW:

01 **Range residency assumption**
Checking if data is from a range-resident animal

02 **Movement models**
Selecting the best-fit movement model through model selection

03 **Home range estimation**
Reconstructing range distribution from sampled locations

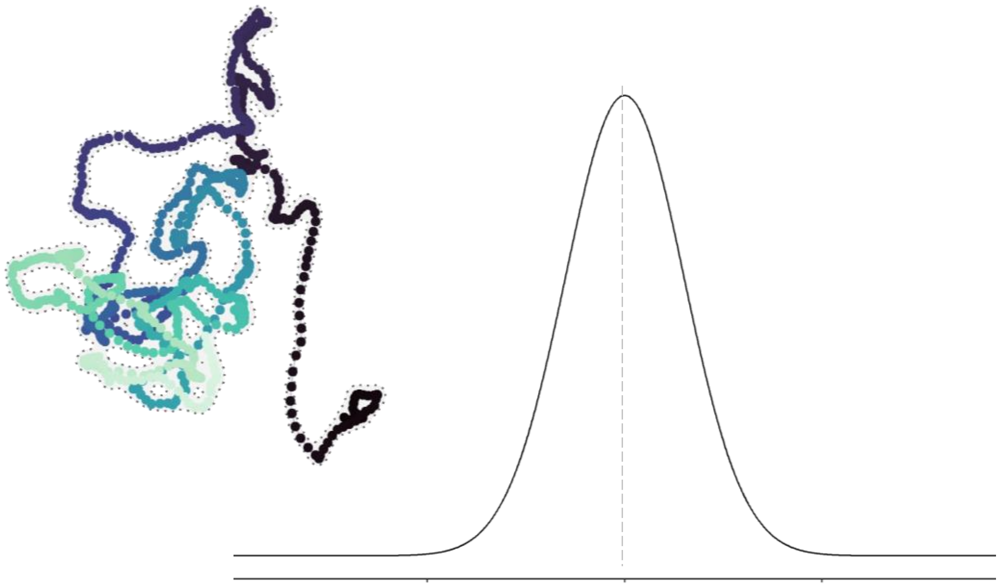
04 **Mitigation measures**
Accounting for common biases in animal movement data

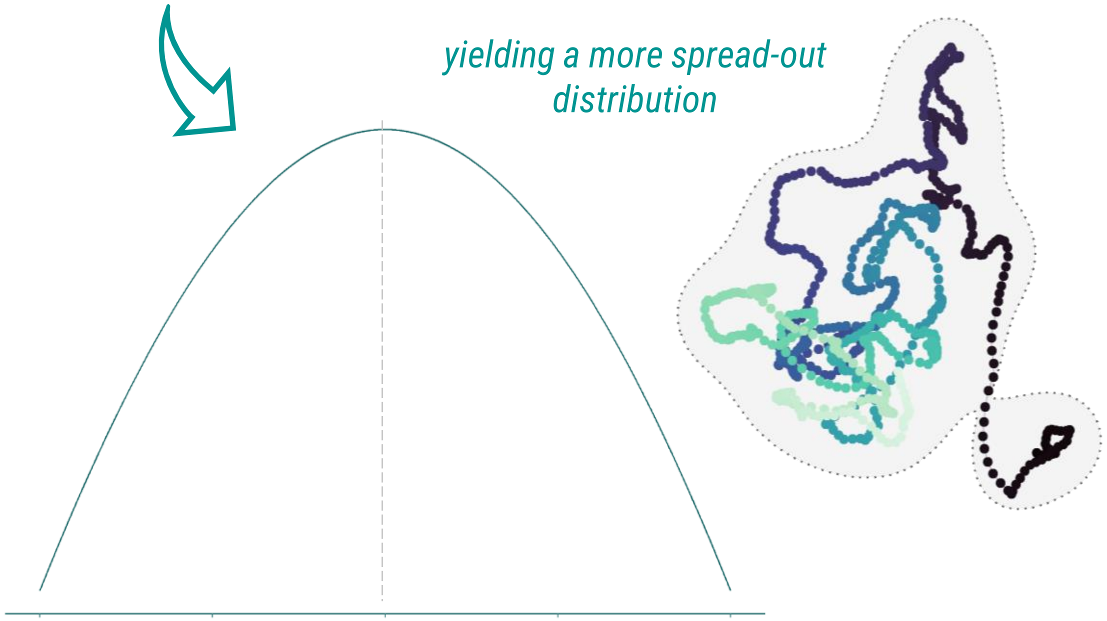
MITIGATION MEASURES

Area-corrected AKDE or **AKDE_C**

Deals with: *oversmoothing*

Even when we account for autocorrelation, GRF-KDEs remain biased due to the natural tendency of the GRF approximation to *oversmooth*.





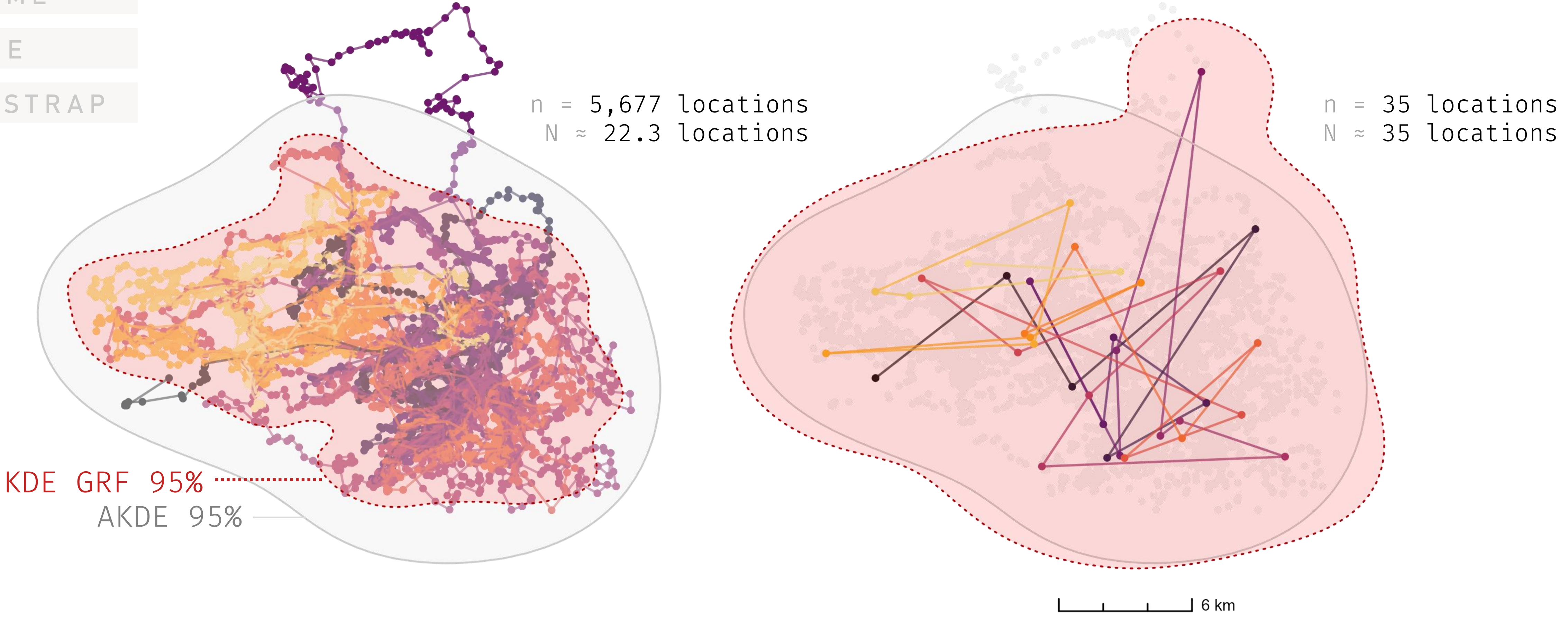
MITIGATION MEASURES

$AKDE_C$

PHREML

wAKDE

BOOTSTRAP



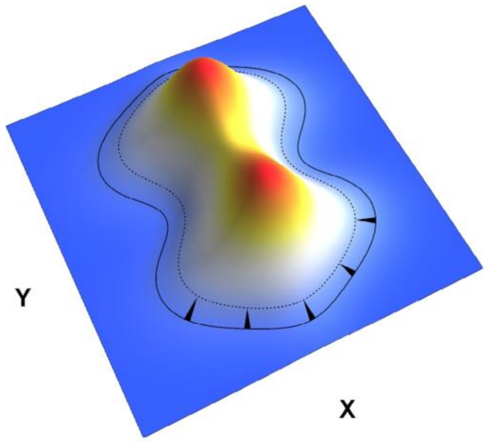
Area-corrected AKDE or **AKDE$_C$**

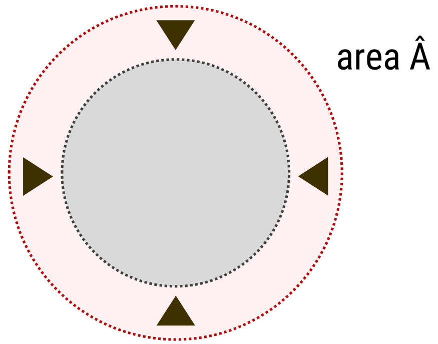
Deals with: *oversmoothing*

Even when we account for autocorrelation, GRF-KDEs remain biased due to the natural tendency of the GRF approximation to *oversmooth*.

Derived an improved (A)KDE that pulls the contours of the location distribution estimate inward towards the data without distorting its shape.

Fleming & Calabrese (2017)
DOI: 10.1111/2041-210X.12673





AKDE$_C$

PHREML

wAKDE

BOOTSTRAP

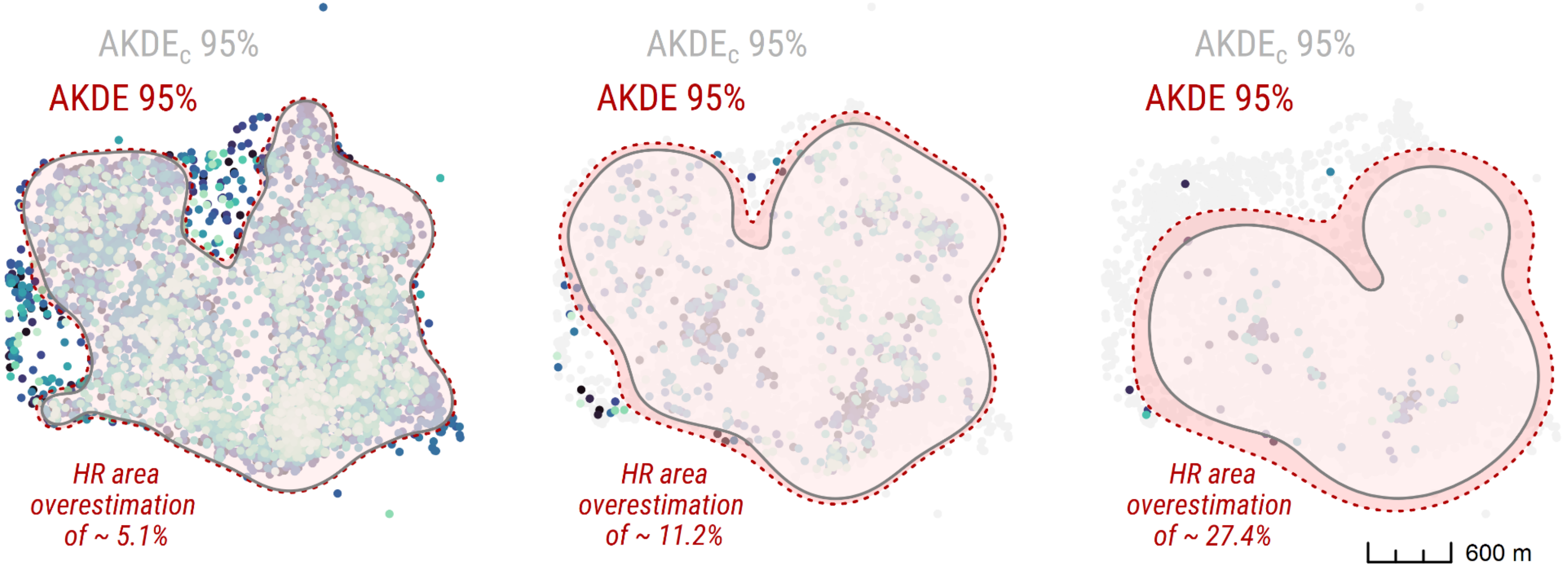
Area-corrected AKDE or **AKDE$_C$**

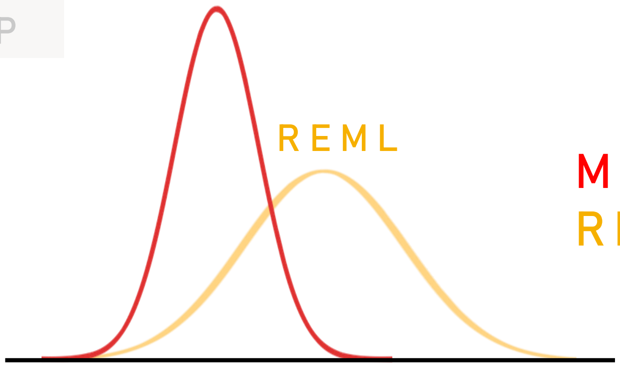
Deals with: *oversmoothing*

Large effective sample size · Sampling duration ≈ 1 year

Medium effective sample size · Sampling duration ≈ 3 months

Small effective sample size · Sampling duration ≈ 15 days





pHREML AKDE

Deals with: *autocorrelation estimation bias*

For optimal performance, we need to estimate autocorrelation correctly.

ML — performs poorly at small sample sizes.

REML — performs poorly at small *effective* sample sizes.

AKDEC
PHREML
wAKDE
BOOTSTRAP

pHREML AKDE

Deals with: *autocorrelation estimation bias*

For optimal performance, we need to estimate autocorrelation correctly.

ML — performs poorly at small sample sizes.
REML — performs poorly at small *effective* sample sizes.

As such, we consider other parameter estimation methods:

perturbative REML (pREML)
Hybrid REML (HREML)
perturbative Hybrid REML (pHREML)

Fleming *et al.* (2019)
DOI: 10.1111/2041-210X.13270

MITIGATION MEASURES

pHREML AKDE

Deals with: *autocorrelation estimation bias*

For optimal performance, we need to estimate autocorrelation correctly.

ML — performs poorly at small sample sizes.
REML — performs poorly at small *effective* sample sizes.

As such, we consider other parameter estimation methods:

Focus on:

small *effective* sample sizes — *perturbative* REML (pREML)
small *absolute* sample sizes — *Hybrid* REML (HREML)
small *absolute* and *effective* sample sizes — *perturbative Hybrid* REML (pHREML)

Fleming *et al.* (2019)
DOI: 10.1111/2041-210X.13270

pHREML AKDE

Deals with: *autocorrelation estimation bias*

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perturbative Hybrid REML (pHREML)

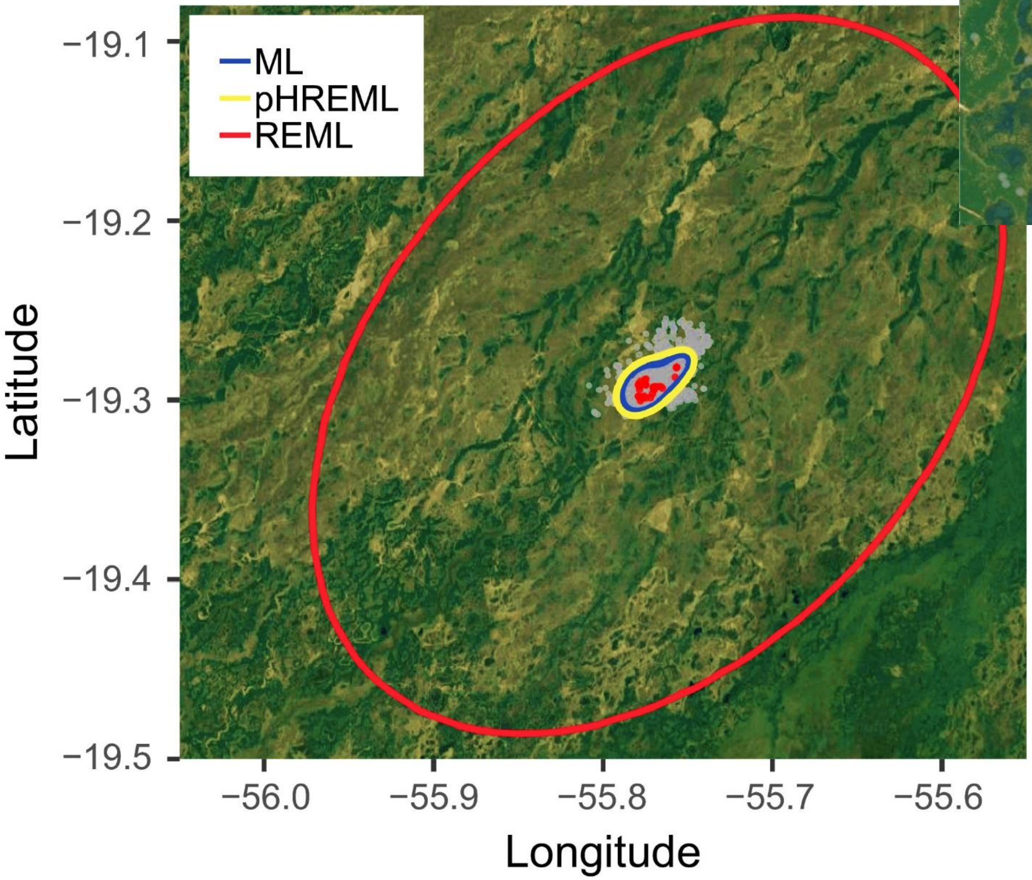
Fleming *et al.* (2019)
DOI: 10.1111/2041-210X.13270

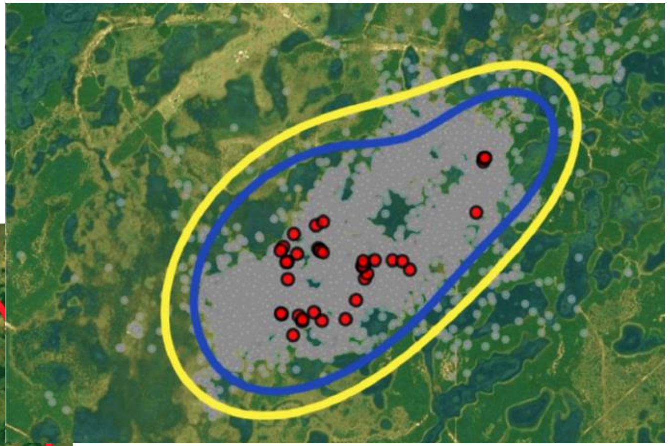
MITIGATION MEASURES

Tracking data (1-hr intervals for 19 months), truncated to **2 days**.

LOWLAND TAPIR

TAPIRUS TERRESTRIS



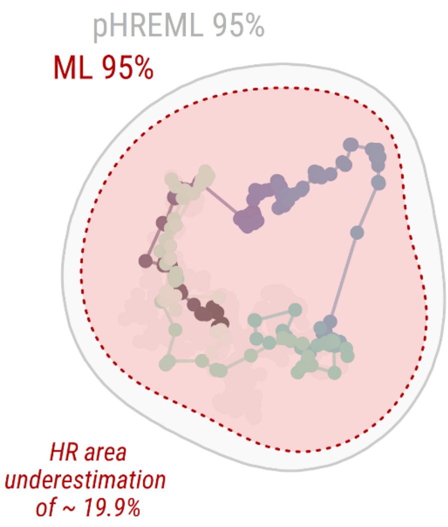


ML
REML
pHREML

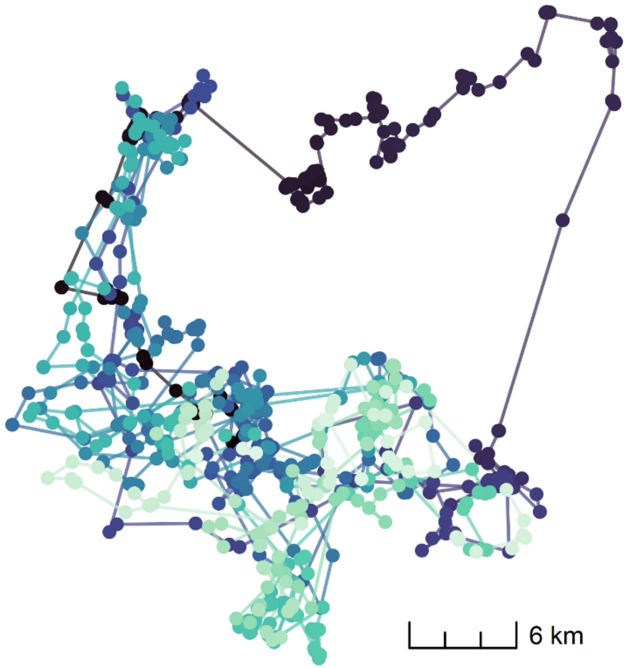
pHREML AKDE

Deals with: *autocorrelation estimation bias*

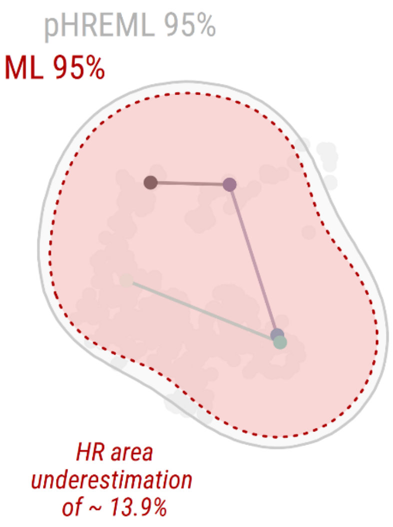
Large absolute &
Small effective sample size
$n = 363 \quad N \approx 3.1$



$n = 1010 \quad N \approx 14.5$



Small absolute &
Small effective sample size
$n = 5 \quad N \approx 4$



Weighted AKDE or **wAKDE**

Deals with: *unrepresentative sampling in time*

- Many real-world issues can lead to *irregular sampling*:

  duty-cycling tags to avoid wasting battery,
  acceleration-informed sampling,
  device malfunction,
  habitat-related signal loss,
  and other causes.

- Shifting *sampling schedules* (based on behavioral or seasonal patterns) is also a common strategy.

wAKDE optimally ***upweights*** observations that occur during *under-sampled times*, while optimally ***downweighting*** observations occurring during *over-sampled times.*

Weighted AKDE or **wAKDE**

Deals with: *unrepresentative sampling in time*

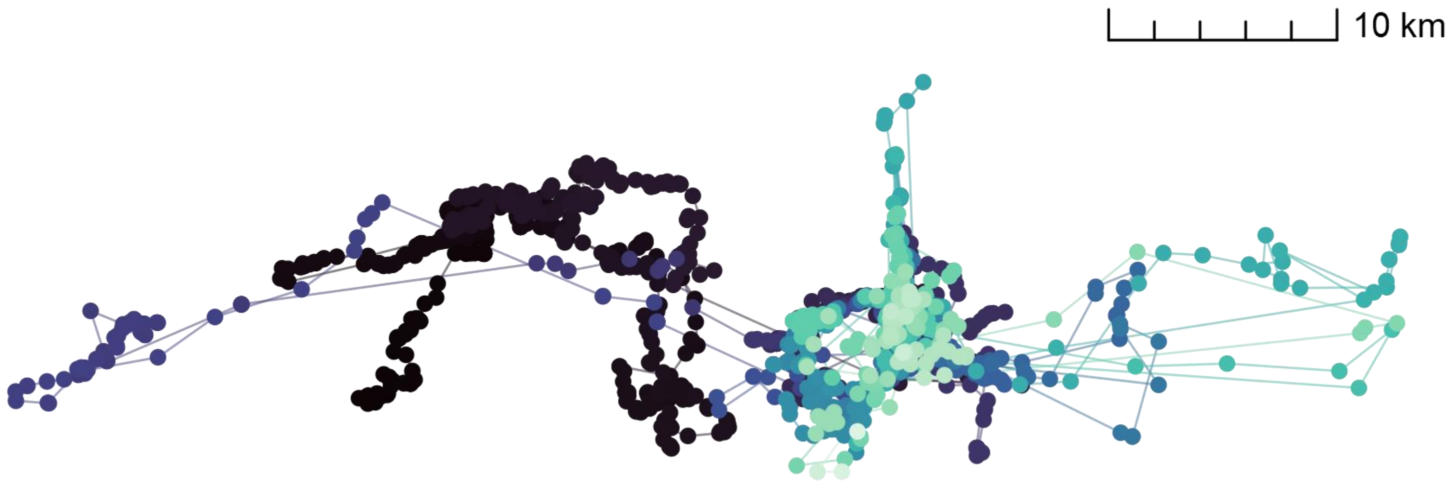


Fig.
African buffalo dataset (nicknamed "Pepper") with an irregular sampling schedule.

AKDEC
PHREML
wAKDE
BOOTSTRAP

Weighted AKDE or **wAKDE**

Deals with: *unrepresentative sampling in time*

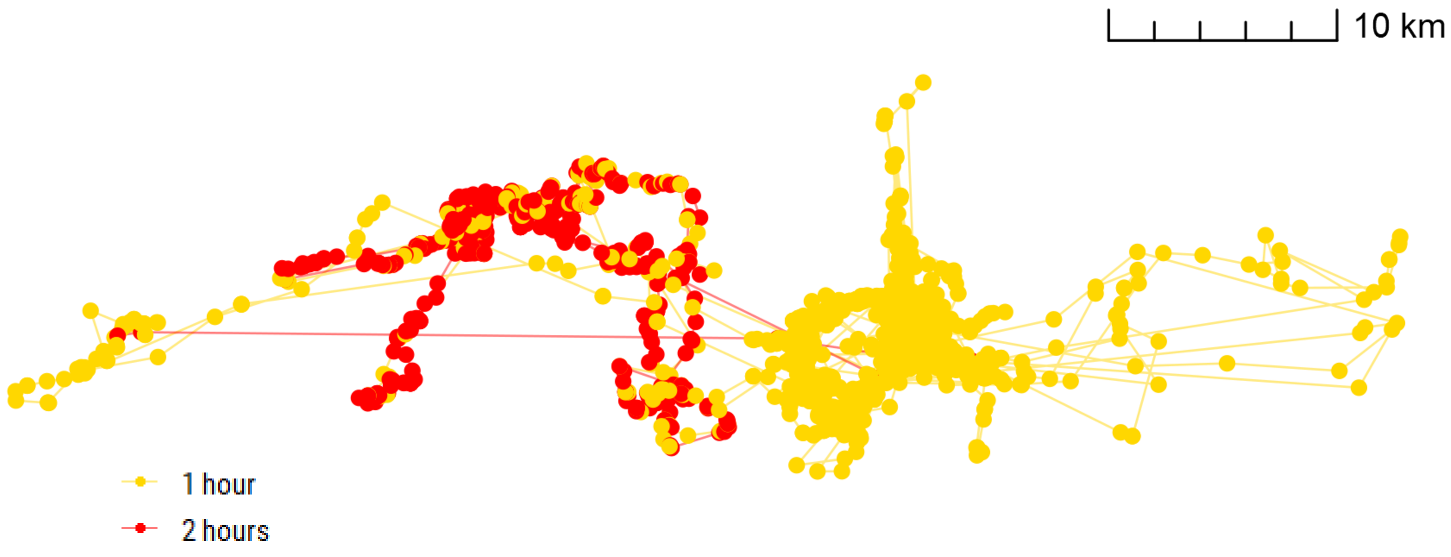


Fig.
African buffalo dataset (nicknamed “Pepper”) with an irregular sampling schedule. Sampling rate shifted from 1 fix every hour to 1 fix every 2 hours.

Weighted AKDE or **wAKDE**

Deals with: *unrepresentative sampling in time*

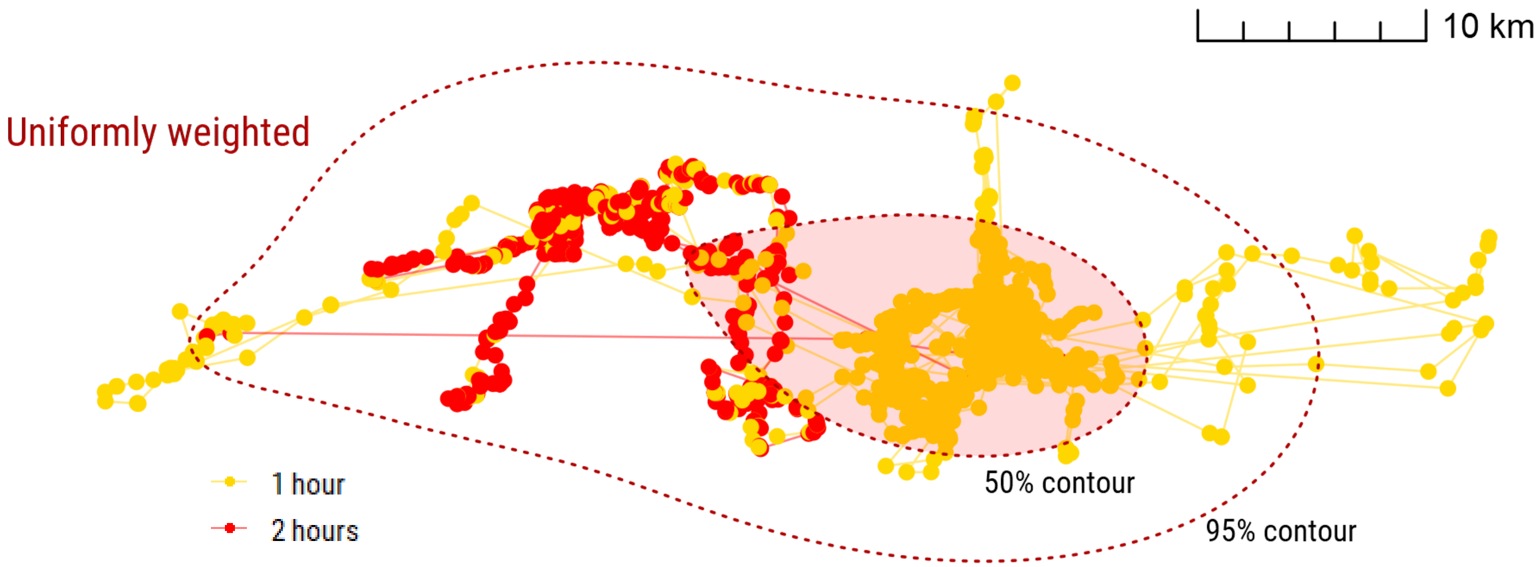


Fig.
African buffalo dataset (nicknamed "Pepper") with an irregular sampling schedule. Sampling rate shifted from 1 fix every hour to 1 fix every 2 hours.

Weighted AKDE or **wAKDE**

Deals with: *unrepresentative sampling in time*

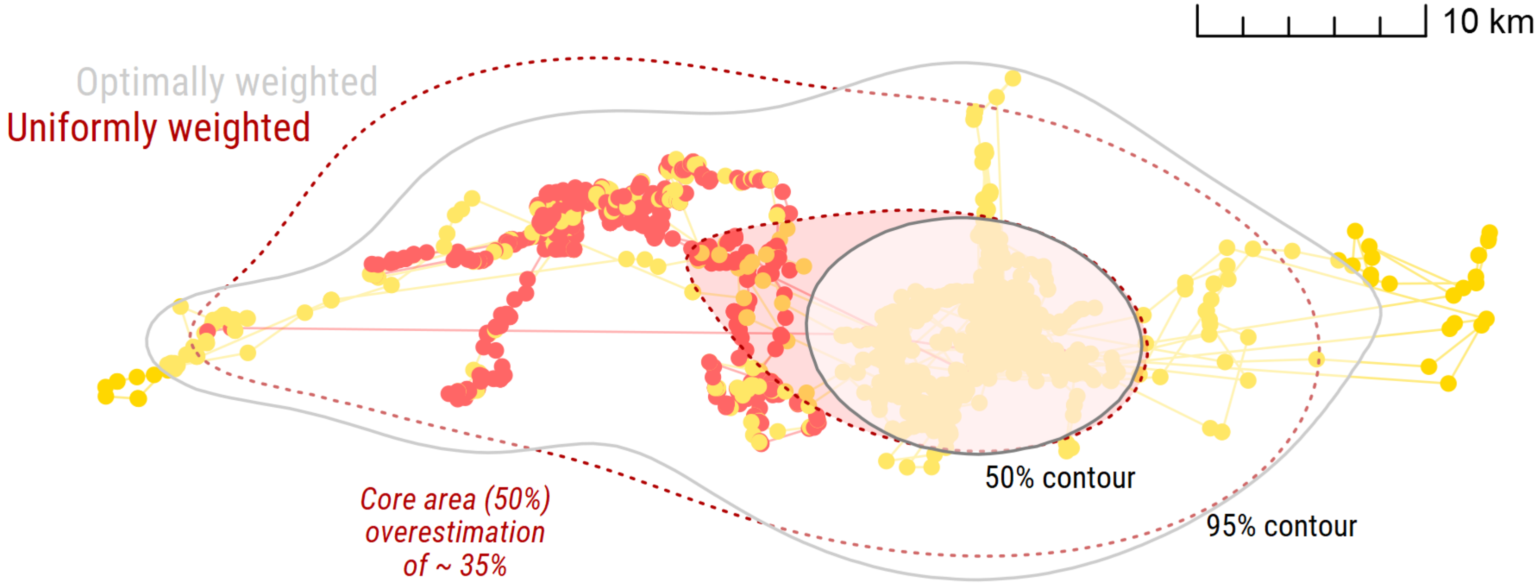


Fig.
African buffalo dataset (nicknamed "Pepper") with an irregular sampling schedule. Sampling rate shifted from 1 fix every hour to 1 fix every 2 hours.

Parametric bootstrapping AKDE

Deals with: *very low effective sample size*

Bartlett (1937)
Residual ML (or REML)

Fleming *et al*. (2019)
perturbative Hybrid REML (pHREML)

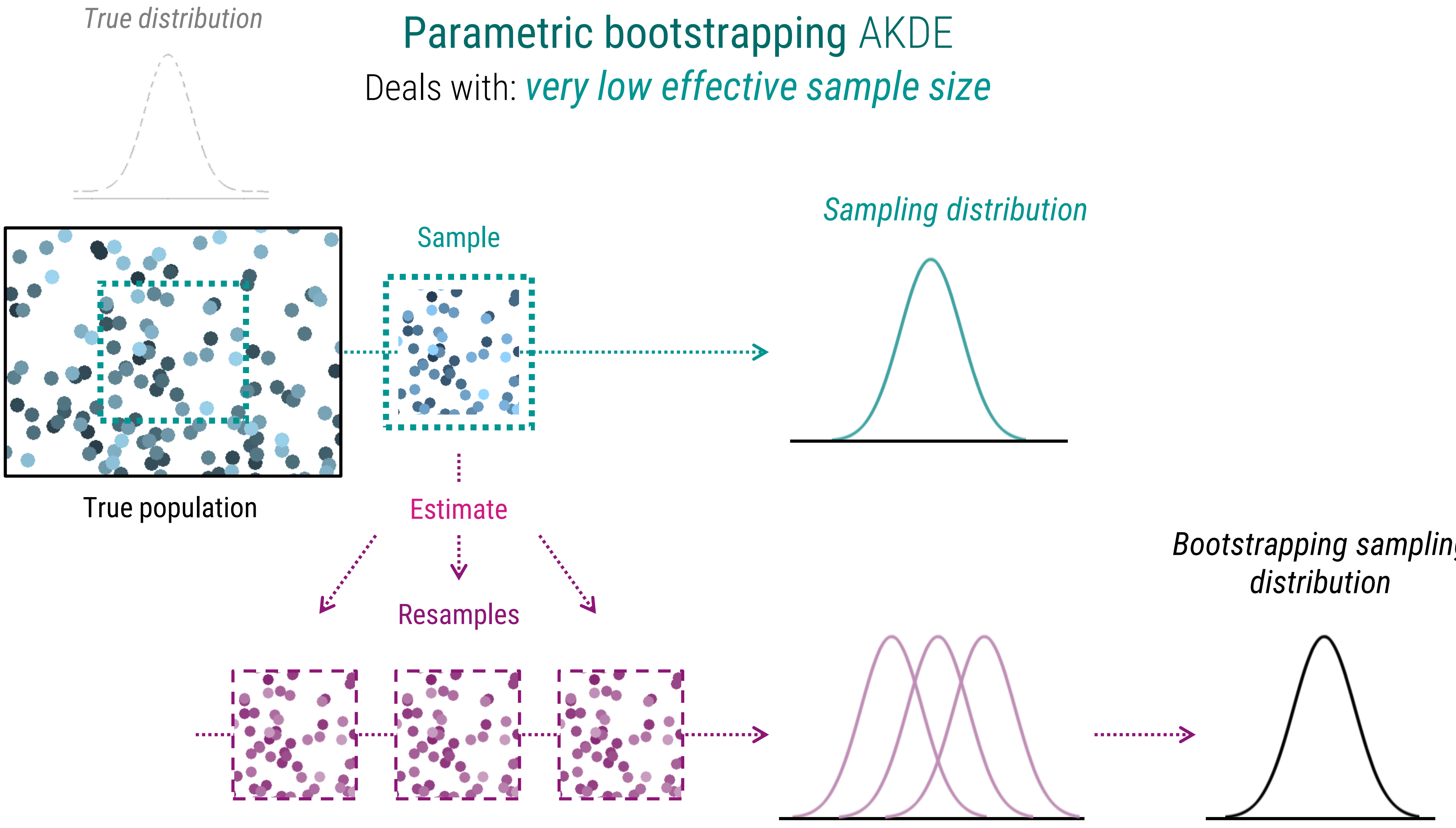
Efron & Efron (1982)
Parametric bootstrapping

The parametric bootstrap estimates the bias and variance of an estimator by *approximating* the sampling distribution of the true movement model with that of the best-fit model.

AKDEC
PHREML
wAKDE
BOOTSTRAP

Parametric bootstrapping AKDE

Deals with: *very low effective sample size*

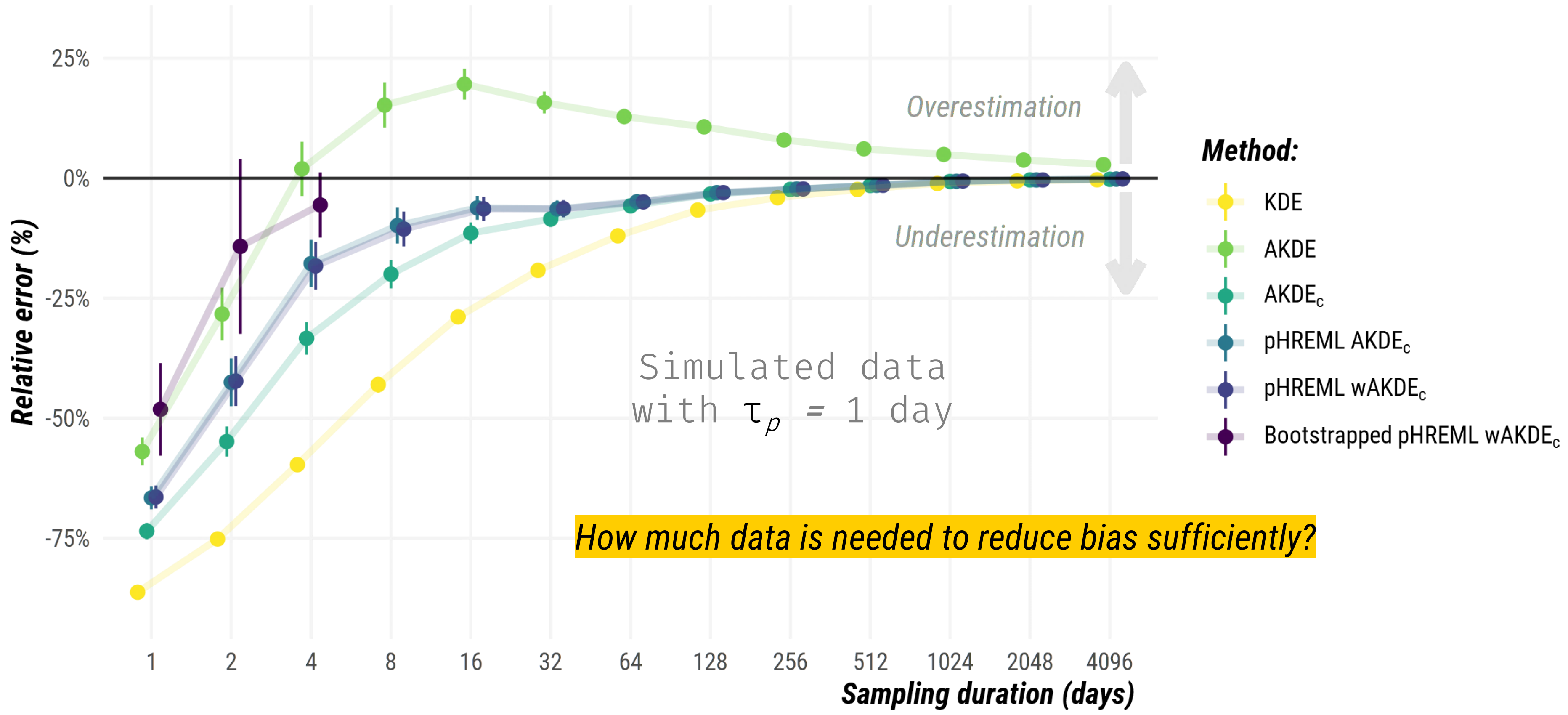


STEP 4

MITIGATION MEASURES

AKDE family

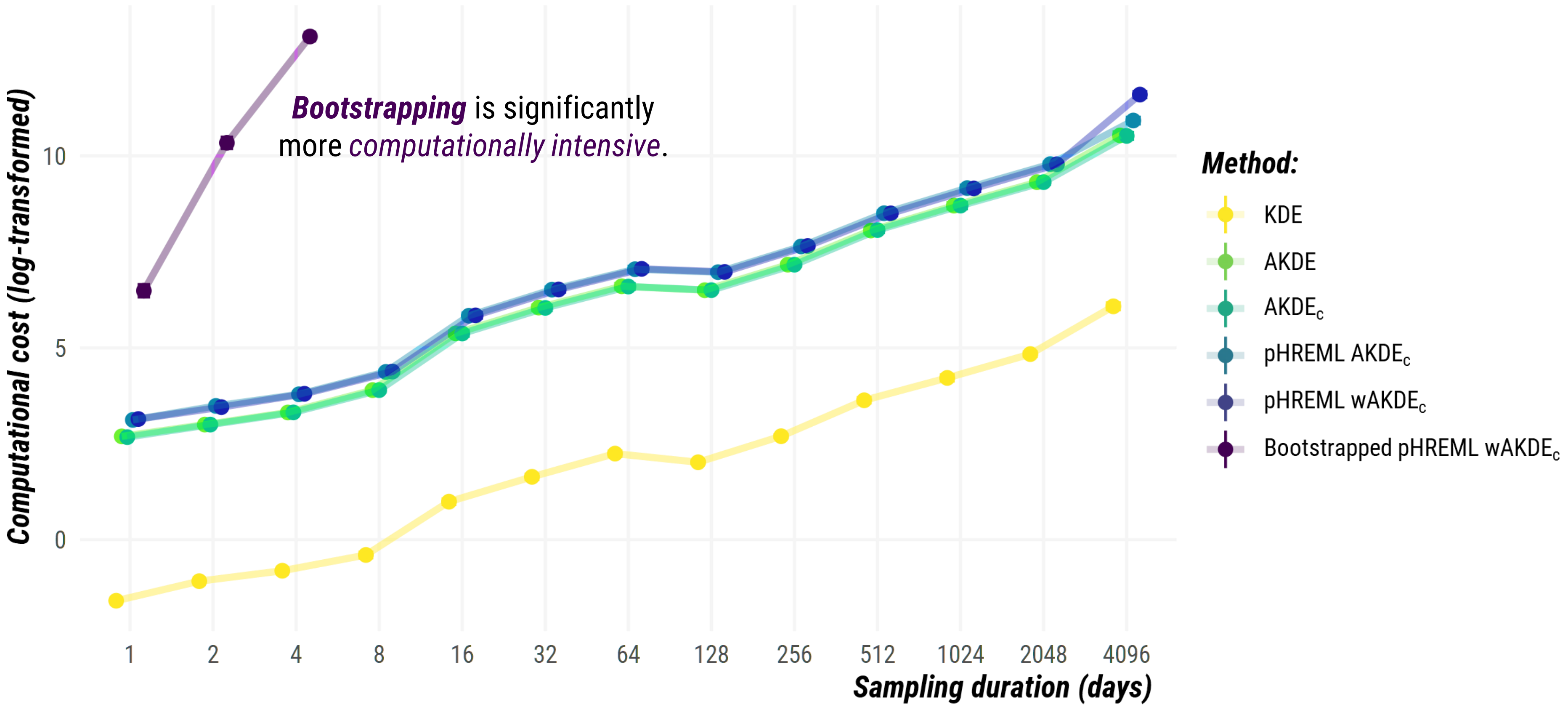
Relative error *versus* sampling duration



How much data is needed to reduce bias sufficiently?

AKDE family

Computational cost *versus* sampling duration



RStudio®

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