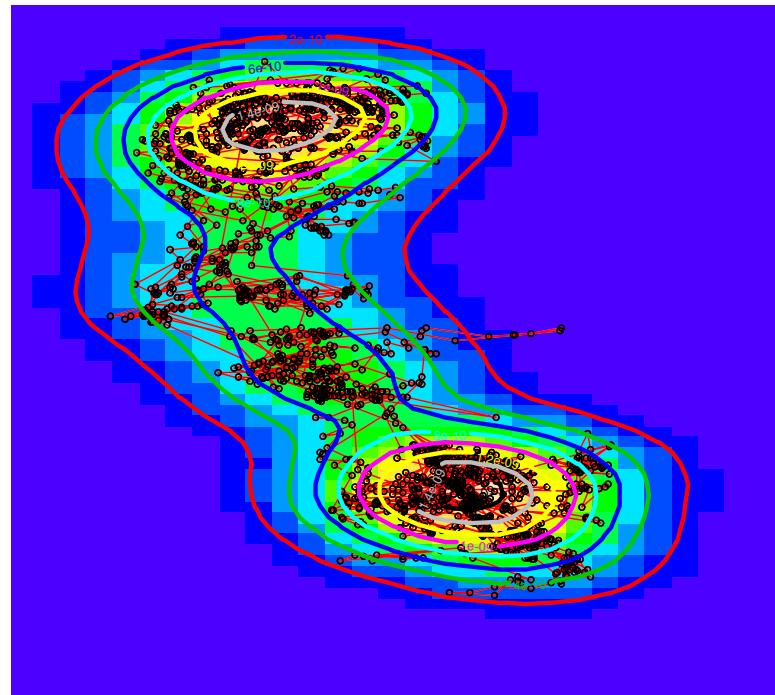


(Statistical) Home Range Analysis



Swansea University
Prifysgol Abertawe

Luca Börger (@lucaborger)
Movement Ecology Workshop
UNESP Rio Claro, 21 March 2018

College of Science
Coleg Gwyddoniaeth

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Plant, Soils, Ecosystems

Movement Ecology

The Movement Ecology group wants to provide a platform for facilitating exchange and collaborations in this wide-ranging, cross-disciplinary field of research.



**MOVEMENT
ECOLOGY
GROUP**

Contact
Secretary: Luca Börger
Co-secretary: Samantha Patrick; Theoni Photopoulou
Blog and Social Media: Move blog, Twitter, Facebook

About us
The Movement Ecology group wants to provide a platform for facilitating exchange and collaborations in this wide-ranging, cross-disciplinary field of research.

About us

The Movement Ecology group wants to provide a platform for facilitating exchange and collaborations in this wide-ranging, cross-disciplinary field of research.

Aims

- (i) Act as a central forum to unite researchers and help clarify conceptual and methodological misconceptions.
- (ii) Attract new Movement Ecology researchers.
- (iii) Guide the development of novel research, especially interdisciplinary research combining technical, computational, and theoretical developments to obtain a refined understanding of the role of organism movements in driving ecological processes.

Upcoming events

We will organise regular meetings, workshops and training initiatives, and online and 'in vivo' events. Details of our upcoming events will be coming soon!

Committee members

- Secretary: Luca Börger
- o-secretary: Samantha Patrick; Theoni Photopoulou
- Deputy secretary: Jonathan Potts
- Treasurer: Garrett Street
- Early careers & training rep: Marie Auger-Méthé
- Industry liaison: Luca Börger
- Events/workshops rep: Hawthorne Beyer; Jonathan Potts
- Communications rep & online resources: Hamish Campbell; Theoni Photopoulou

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BES Movement Ecology Published by Hamish Campbell [?] · Yesterday at 10:54 ·

Fancy a post-doc in Australia.
The Movement and Landscape Ecology Lab at Charles Darwin University, Darwin is seeking a highly motivated researcher to undertake ecological studies upon the highly mobile Gouldian finch within the Kimberly region of Northern Australia. The successful applicant will investigate the role fire plays on the movement ecology of this endangered species, and the consequential impact upon breeding success. Duties include, the development and deployment... See more

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<http://viz.icaci.org/Lorentz2017/>

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Luca Börger 4 February 2017 at 17:08 ...



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MOVEMENT ECOLOGY GROUP



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United Kingdom
ow.ly/wVoB306W7QE
Joined December 2016

Tweets [Tweets & replies](#)

 BES Movement Ecology Retweeted
Garrett Street @street_ecology · Jan 31
Can population growth induce an ideal-free distribution in non-ideal dispersive animals? [@BritishEcoSoc](#) [@BES_Move_SIG](#) [@WileyOpenAccess](#)



Dynamical facilitation of the ideal free distribution...
The ideal free distribution (IFD) requires that individuals can accurately perceive density-dependent habitat quality, while failure to discern quality differences below...

onlinelibrary.wiley.com

1 2 6

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Worldwide trends

#UELdraw 12.7K Tweets
#BuenViernes 5,023 Tweets

BES Movement Ecology SIG

Upcoming events 2018

Movement Ecology Workshop
U. British Columbia - Vancouver
18 - 22 June 2018

Marie Auger-Methier, Garrett Street, Luca Borger

Movement Ecology SIG Annual Meeting
Swansea University – Luca Borger
29 June 2018

Movement Ecology ISEC Social Event
03 July 2018

Juan Morales et al.
Theoni Photopoulos

Movement Ecology Early Career Researcher Workshop
September 2018 - Chicheley Hall

Event will focus on early-career researcher professional development. Workshop content will focus on both key movement ecology methods (with computer practicals) as well as the cross disciplinarity of their research, with examples from key note lecturers how they developed from one area of movement ecology to another; discussions on foundational concepts and methods in Movement Ecology and effective networking, and "Lightning Talks" (2-3 minute talks by attendees); practical sessions on grant/fellowship applications development; and academic and non-academic routes in movement ecology.

Samantha Patrick (Liverpool); Garrett Street (USA); Luca Borger (Swansea)



BES Movement Ecology

Home range studies: why so messy?

Statistical Consultant Approach

Step 1: Elicit research questions.

Step 2: Translate questions and hypotheses into quantifiables (statistical models and parameters).

Step 3: Determine study design and analysis strategy (→ Methods).

Step 4: Fit models to movement data.

Step 5: Evaluate model fit and derive inferences.

Home range studies: why so messy?

...what usually happens...

- Capture as many animals as possible, collect location data.
- How much data do I need?
- MCP or KDE...bandwidth???
- Autocorrelation?
- Estimate HRs, then...
- Ask, what are the implications of these HR estimates for my study species?

→ No, no, no, please don't! Questions first, then Methods.

Extreme focus on methods - WHY?

- There are lots of “methods” reviews, comparisons among estimators, and critiques of “methods reporting”
- Often conflicting advice regarding sample size, autocorrelation, estimation methods.
- Little to no discussion of how the estimates are used (i.e., the motivating question(s))

QUESTIONS FIRST!

Often, home ranges are estimated because the researcher has not carefully designed the research being conducted and/or no hypothesis was originally designed to be tested (White & Garrot 1990). “poor substitute for good experimental design”

Often, home ranges are estimated because the researcher has not carefully designed the research being conducted and/or no hypothesis was originally designed to be tested.

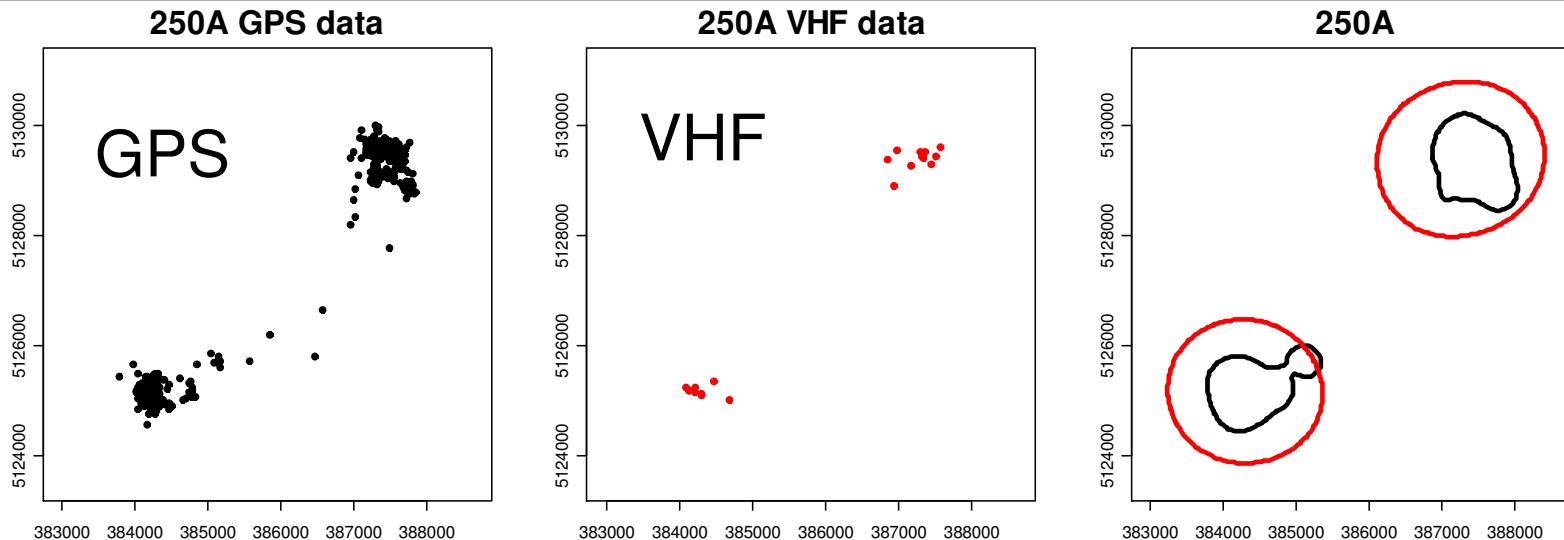
(White & Garrot 1990)

“poor substitute for good experimental design”

Examples of motivating questions

- Why or under what conditions do animals choose to have a home range?
- How much area does species x require?
 - Conservation reserve planning
- What determines animal space use patterns and ultimately HR size?
 - Across species comparisons: scaling with body size
 - Within-species comparisons: individual-based and habitat-based characteristics

Examples of motivating questions



Kochanny et al. (2009) J. Wildl. Manage.

- Where can I generally find this animal?
- What path is taken between the 2 clusters of obs?
- How big of an area does this animal use to meet its daily needs? Reserve design or within-species variation?
- To determine impact of sampling, need to know the question!

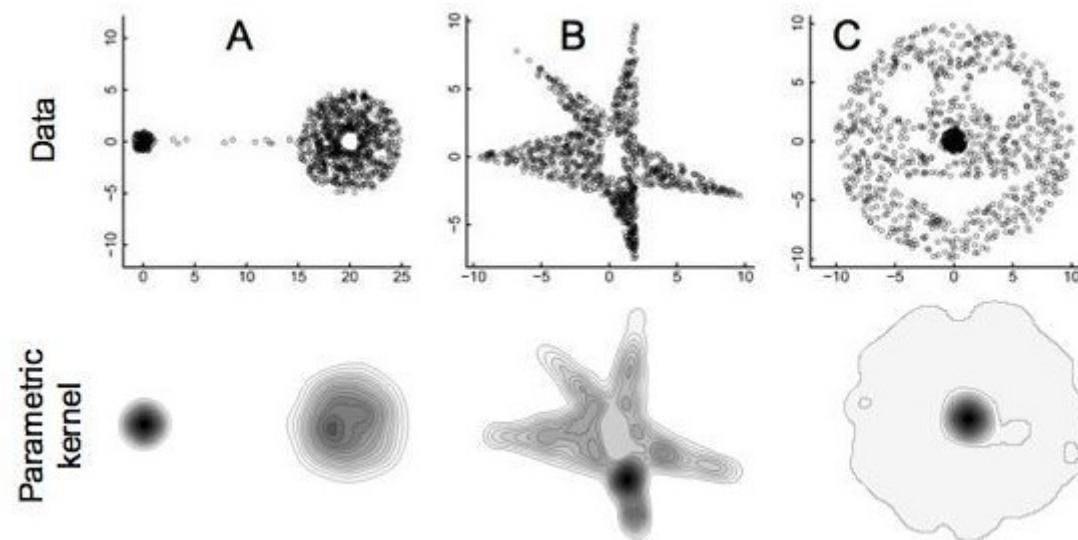
Fieberg & Börger (2012) J. Mammal.
Börger et al. (2006) J. Anim. Ecol.

Examples of motivating questions

Where “exactly” can I find this animal?

- Common criticism of MCPs and KDEs (including unused/inaccessible areas)
- Common example of methods papers that uses extreme cases and unsupported statements to boost own new method...

Getz et al. (2007 PlosOne)



Fieberg & Börger (2012) J. Mammal.

Examples of motivating questions

When building a conservation reserve,
how much area is needed?

- Want good estimate of HR size (some bias OK?)
- “HR size” is not a fixed quantity
 - Area requirements will depend on resource availability within the reserve.
- Map resources and think about energetic requirements?
- Try multiple methods

Examples of motivating questions

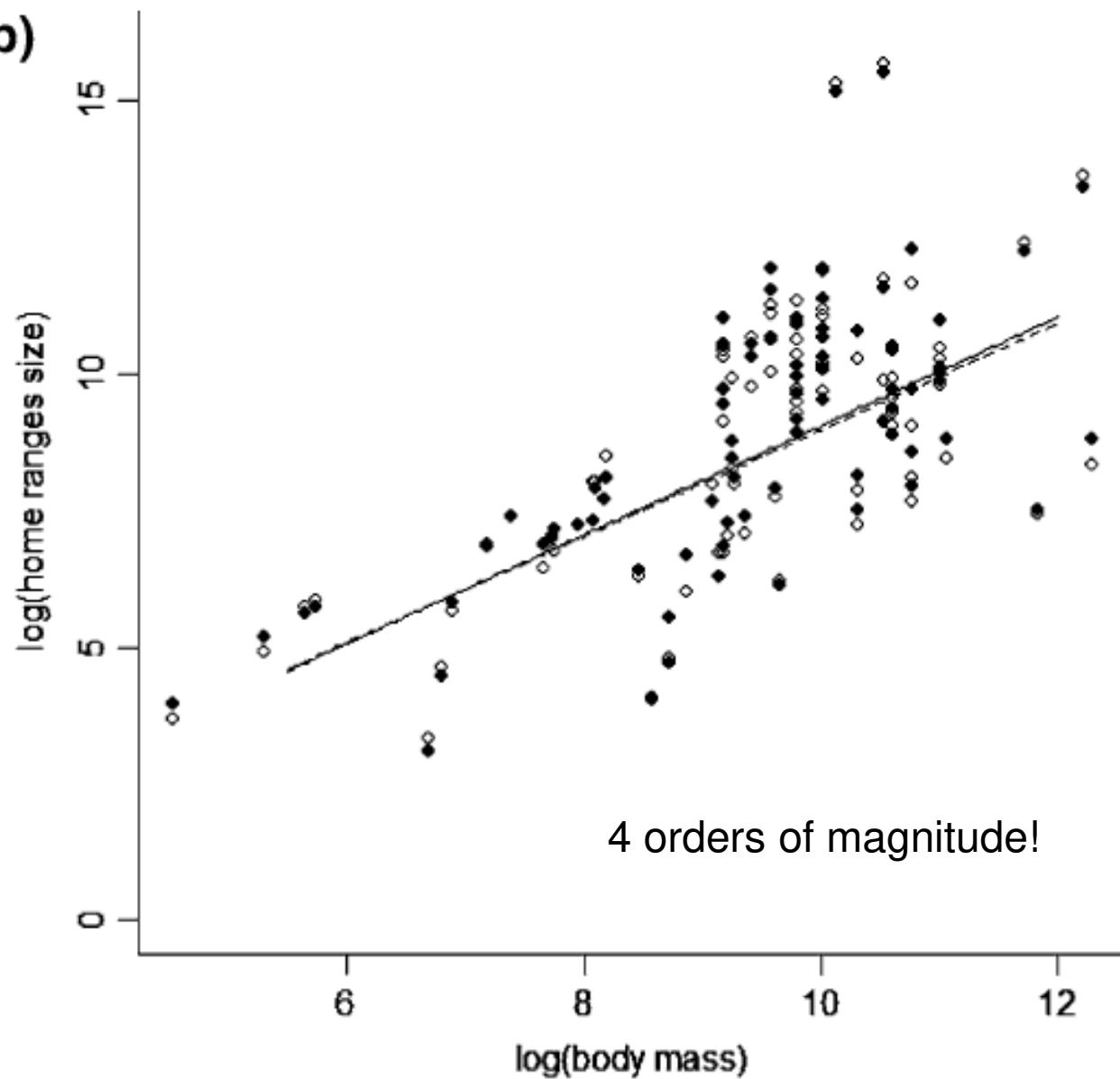
Comparative studies

Bias may be less important than variance / stability → Börger et al. (2006) J. Anim. Ecol.

Nilsen et al. (2008):

- Among-species comparison: choice of home range estimator (MCP versus KDE) made little difference
- Within-species comparisons: choice of estimator explained as much variation as covariates of interest

(b)



Examples of motivating questions

What individual-based and habitat-based characteristics are associated with home range size?

- Number of predictors often \sim = number of animals
- Over-reliance on easily collected GIS data.
- Non-standardized study duration and sampling intensity adds variability.
- Need more focused thinking, more attention to predictions from theoretical ecology

**Temporal unit home range estimates!
Otherwise, as reporting speed without time unit...**

Movement modes

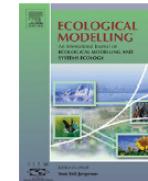
ECOLOGICAL MODELLING 205 (2007) 397–409



available at www.sciencedirect.com



journal homepage: www.elsevier.com/locate/ecolmodel



Home range dynamics and population regulation: An individual-based model of the common shrew *Sorex araneus*

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^a RIFCON GmbH, Breslauer Str. 7, 69493 Hirschberg, Germany

^b UFZ, Helmholtz Centre for Environmental Research – UFZ, Department of Ecological Modelling,
Permoserstr. 15, 04318 Leipzig, Germany

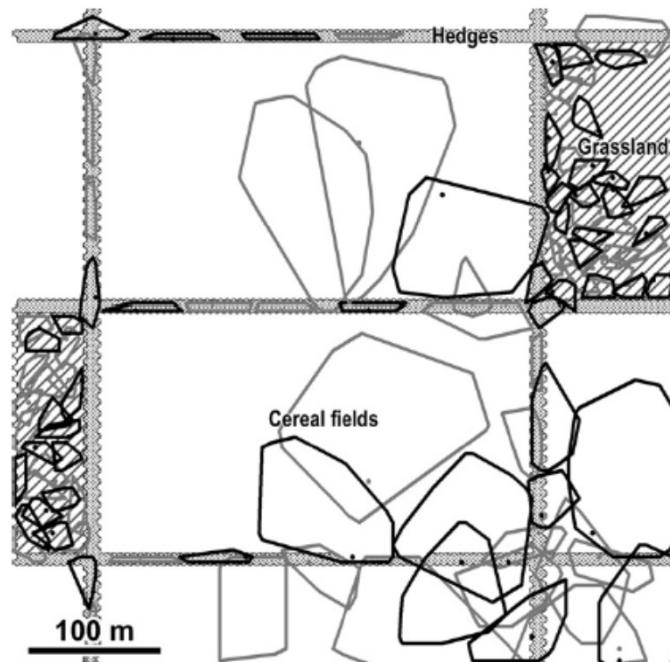


Fig. 5 – Spatial distribution of home ranges in a mixed habitat (25 ha) after a 1-year simulation.

Home range behaviour may not be well understood without considering also dispersal and the dynamic switches home range/dispersal.

Wang & Grimm (2007) Ecol. Model.

What is a home range?

“the area, usually around a home site,
over which the animal normally travels in search of food”

“...that area traversed by the individual in its normal activities of food gathering,
mating, and rearing young.

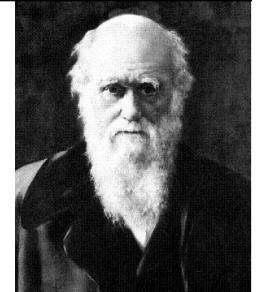
Occasional sallies outside the area, perhaps exploratory in nature,
should not be considered as in part of the home range.

(Burt 1943: 351)

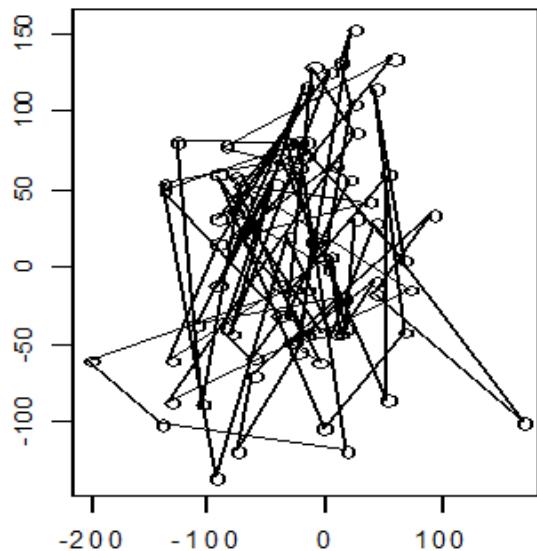
What is a home range

“... most animals and plants keep to their proper homes,
and do not needlessly wander about...”

Charles Darwin (1861) *The origin of species*



→ Site fidelity



What is a home range

- Biological Definition: HR = emergent space use pattern that results from animals restricting their movements within a certain area while attempting to meet their needs for growth, survival, and reproduction (see also Moorcroft & Lewis 2006).

→ HR = index (probe, *sensu* Turchin 1998)

→ not something directly chosen/selected for by an animal ("today I will use 150 ha"....)

- Statistical definition: HR = stationary space use distribution
(see Blackwell 1997).

Sampling design

Finite population sampling perspective

(Otis and White 1999, Fieberg 2007)

- Representative sample
- Biologically meaningful time period

Experimental design perspective

- Aim for contrast in data
- Control for non-interesting effects

The home range need not cover the same area
during the life of the individual Burt (1943)

Sampling design

- Think: sampling duration and sampling intensity rather than sample size.
- Sampling duration influences WHAT.
 - Biologically meaningful time period
 - Life history stages, timing of dispersal and migration events
- Sampling intensity influences how WELL.
 - More data is nearly always better
 - Tradeoffs involving cost, sampling rates, sampling durations
- Sample size is NOT the number of locations, but the number of individuals and the number of time intervals monitored

Hebblewhite & Haydon (2010) Phil. Trans. R. Soc. B
Börger et al. (2006) J. Anim. Ecol.
Fieberg (2007) Ecology

Sampling design

- Worry less about autocorrelation, more about...
- Missing data (e.g. problems locating individuals)
 - Impute or weight data
 - Qualitative assessments
- Variable sampling durations
 - “Seasonal HRs” based on 2 and 4 months(?)
 - Need to think about temporally changing space use patterns

Questions & Biology before Methods

You see? Lots to think about before considering ANY HR estimation method

...let's continue...

Home range vs. Territory

Home range: defined and estimated without reference to defence or advertisement or reaction to intrusion by neighbouring individuals; only the presence of the individual is required.

(Brown & Orians 1970)

Territoriality arises when individuals exhibit spatially oriented aggressive behaviour, i.e. aggressive defence of a space containing limiting resources.

(Burt 1943; Brown & Orians 1970; Davies & Houston 1984)

A territory is estimated by delineating the location of defence events, and the location of competing neighbours is needed to define the area of exclusive use.

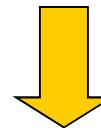
(Burt 1943; Brown & Orians 1970).

Territory \leq Home range

Börger et al. (2008) Ecol. Lett.

From movement path to space use quantification: Probability density function & Utilization distribution

$$u(x,t)$$



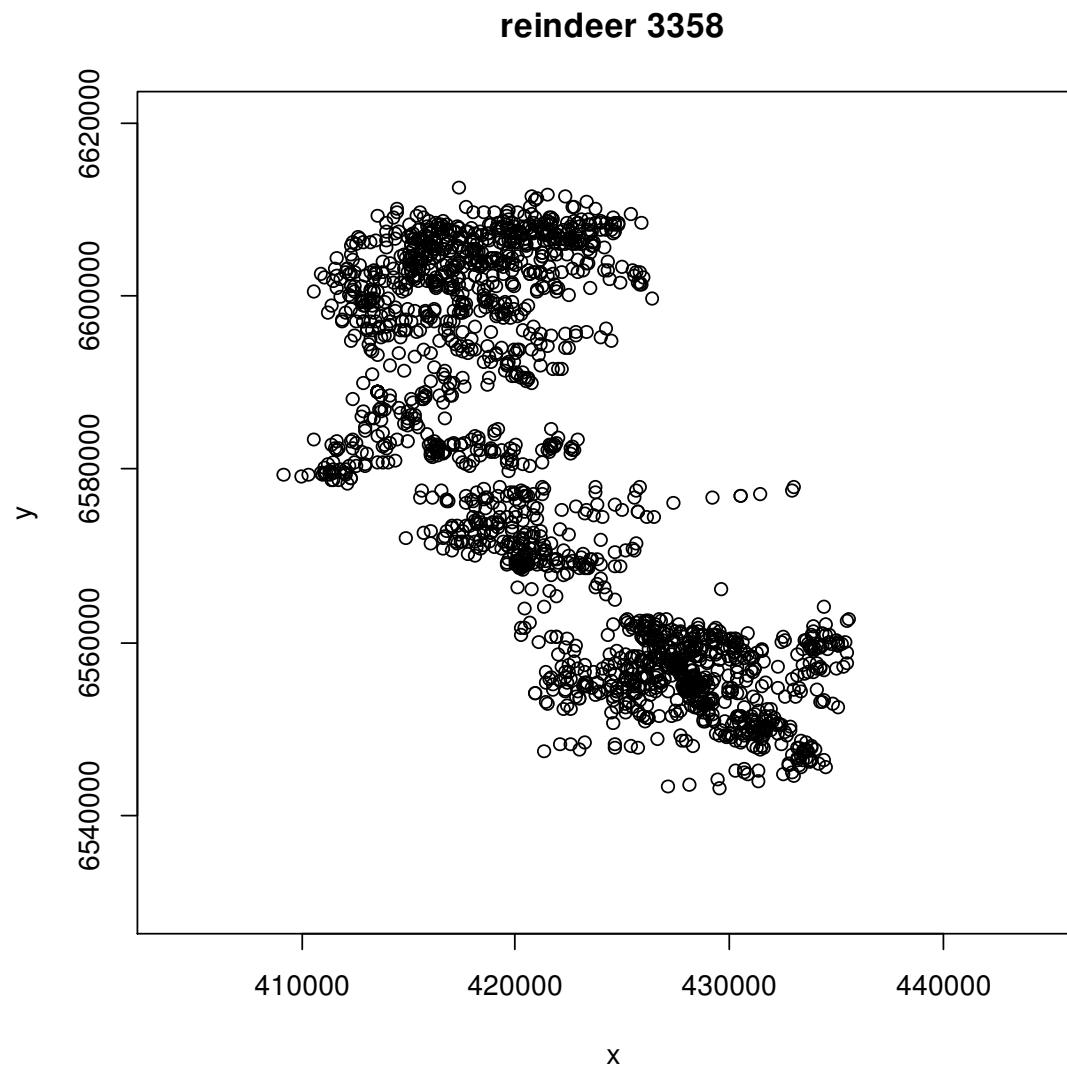
$$\Pr ob\{a \leq X(t) < b\} = \int_a^b u(x,t)dx$$

Utilization distribution function: relative frequency distribution of an animal's location over time

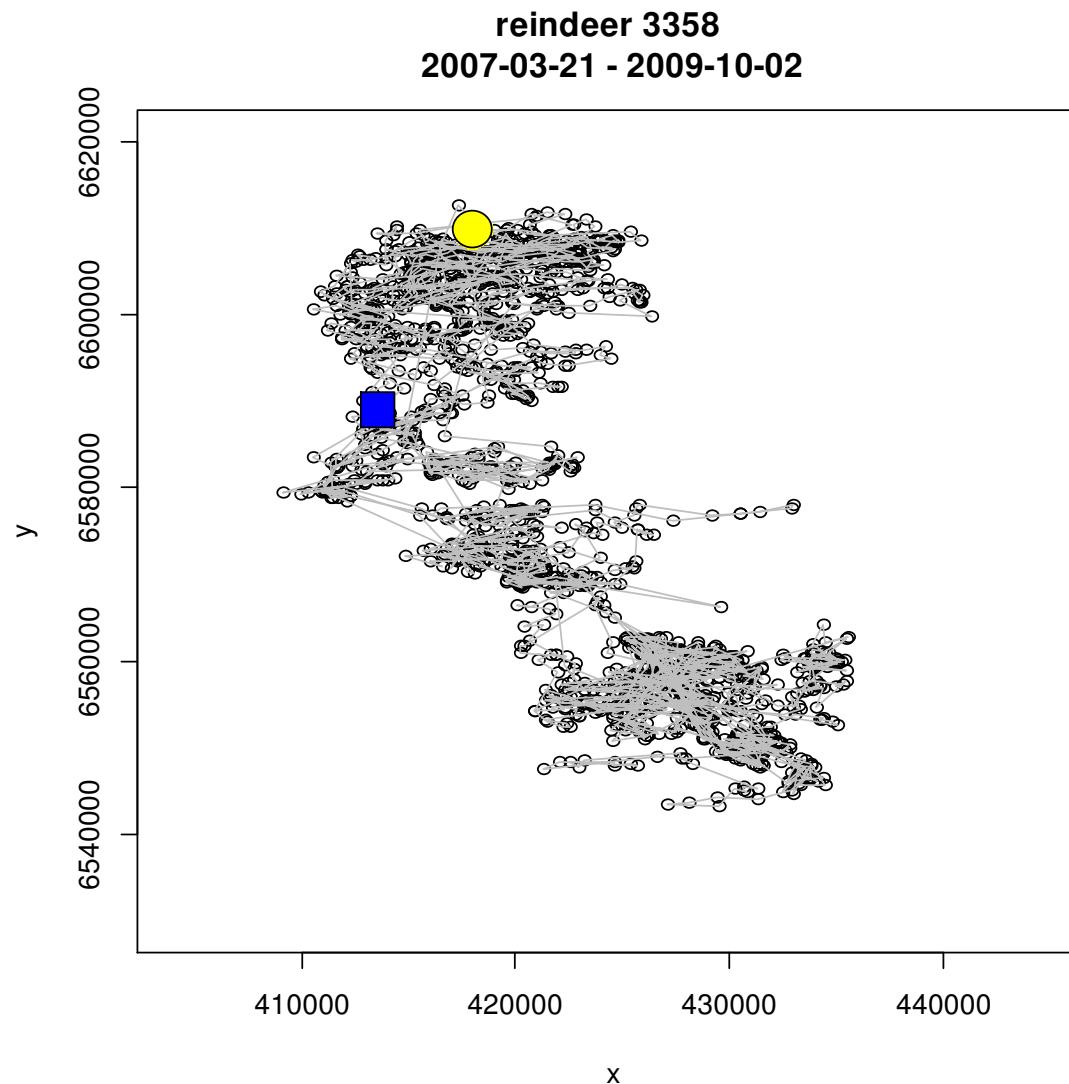
$$f_{UD}(x,y)$$

- Bivariate Probability Density function
- Multivariate extensions (time)

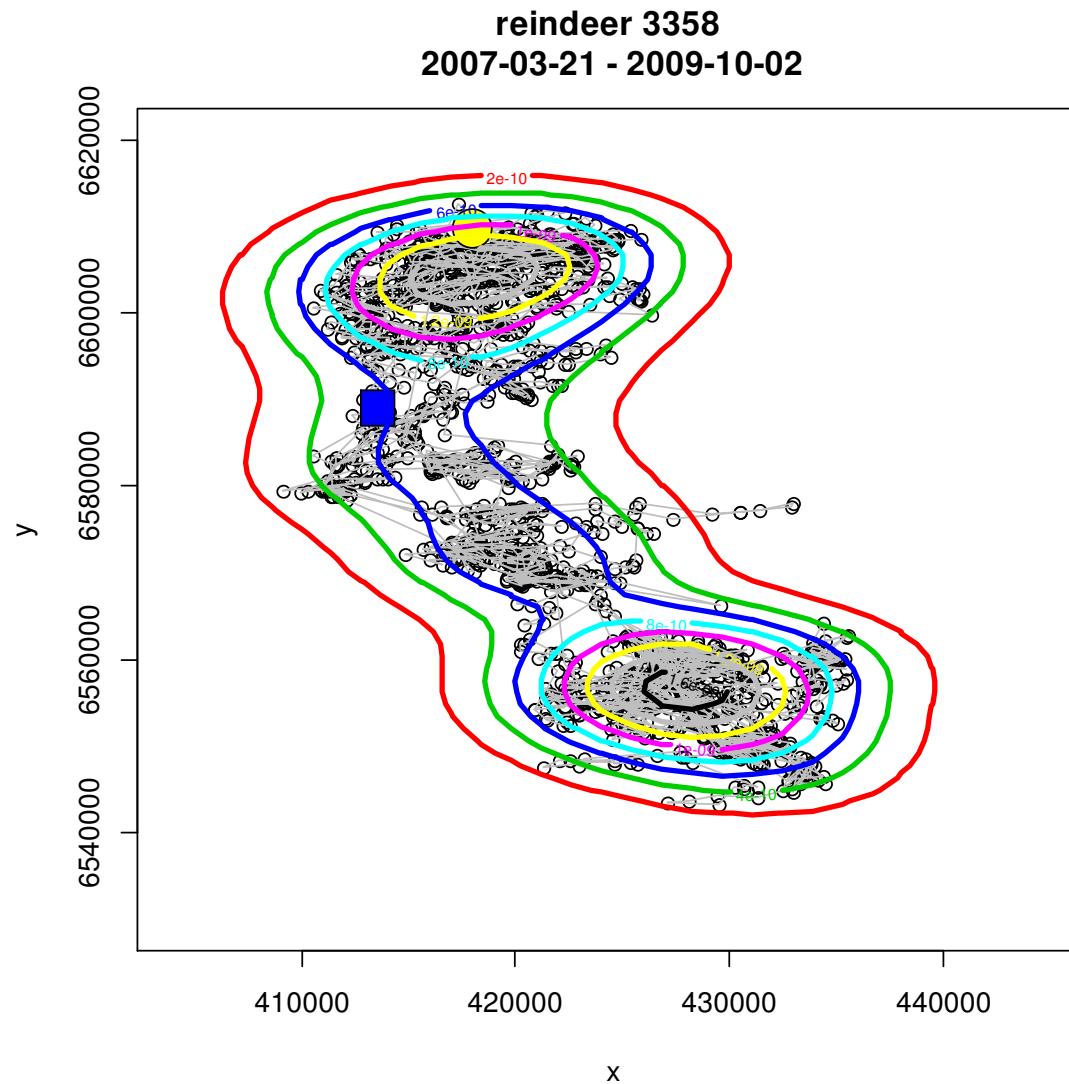
From movement path to space use quantification: Kernel density estimation



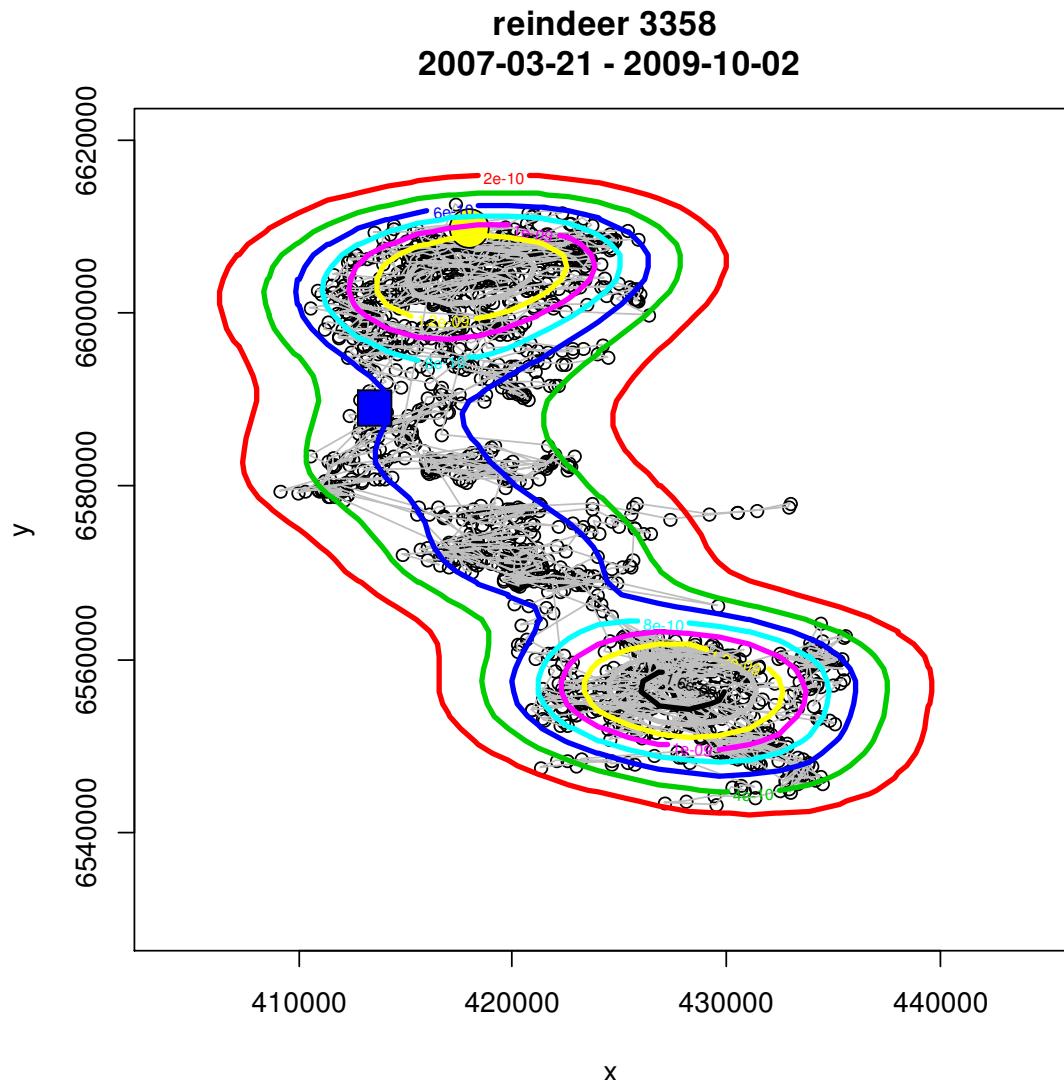
From movement path to space use quantification: Kernel density estimation



From movement path to space use quantification: Kernel density estimation



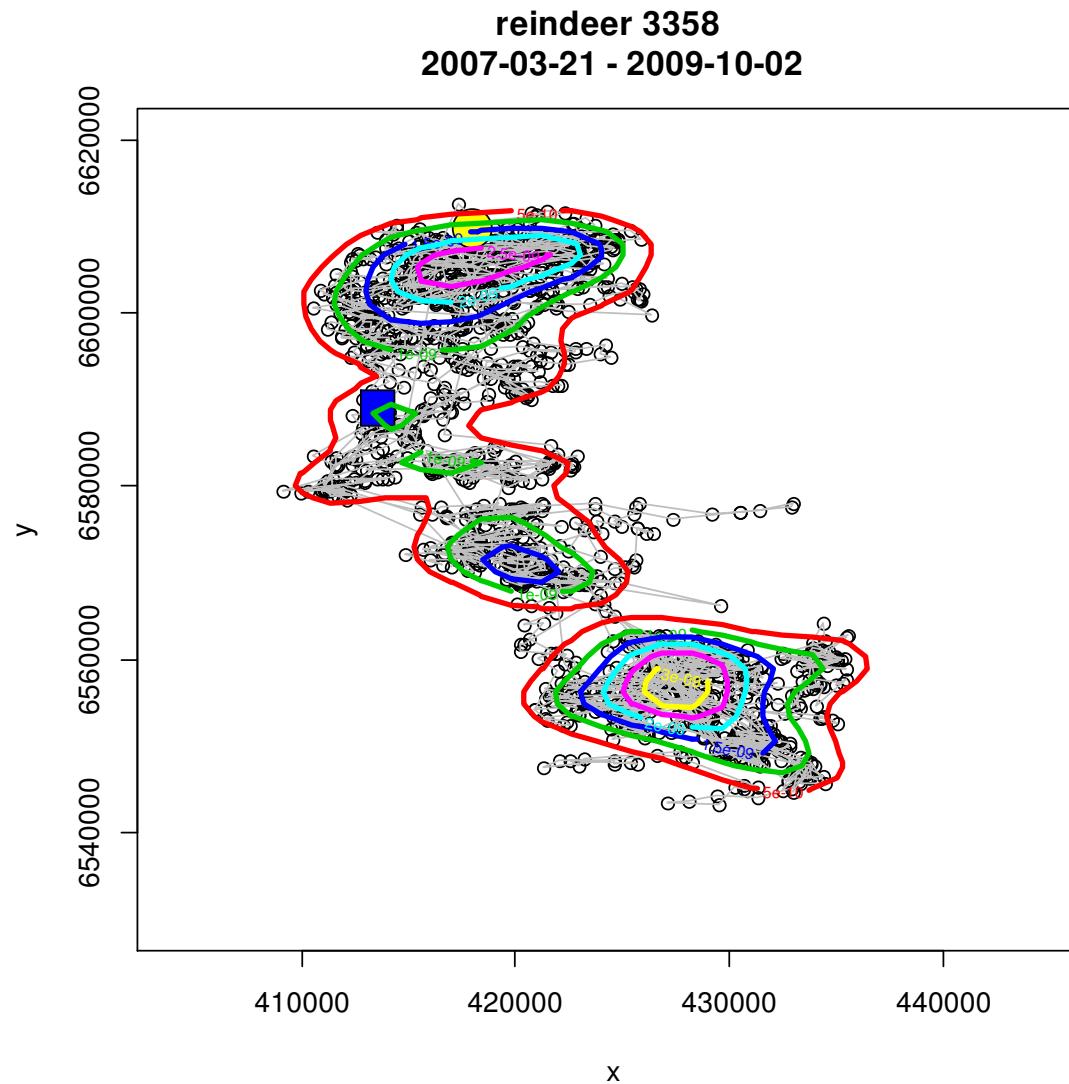
From movement path to space use quantification: Kernel density estimation

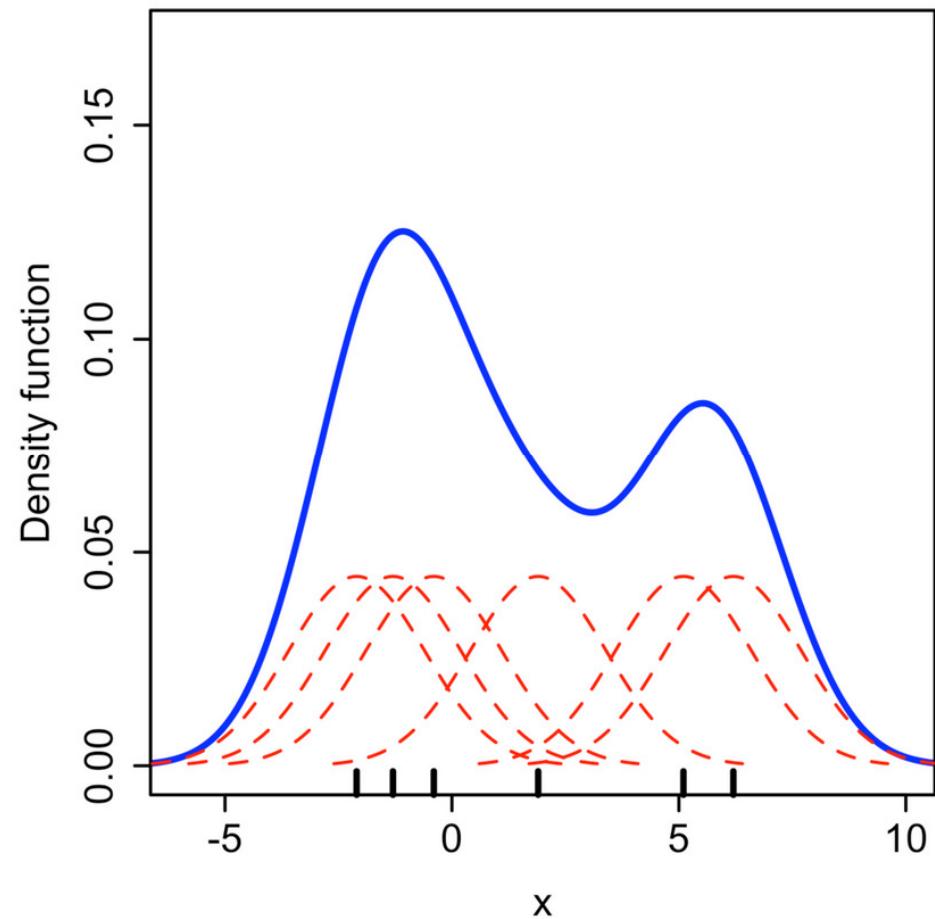
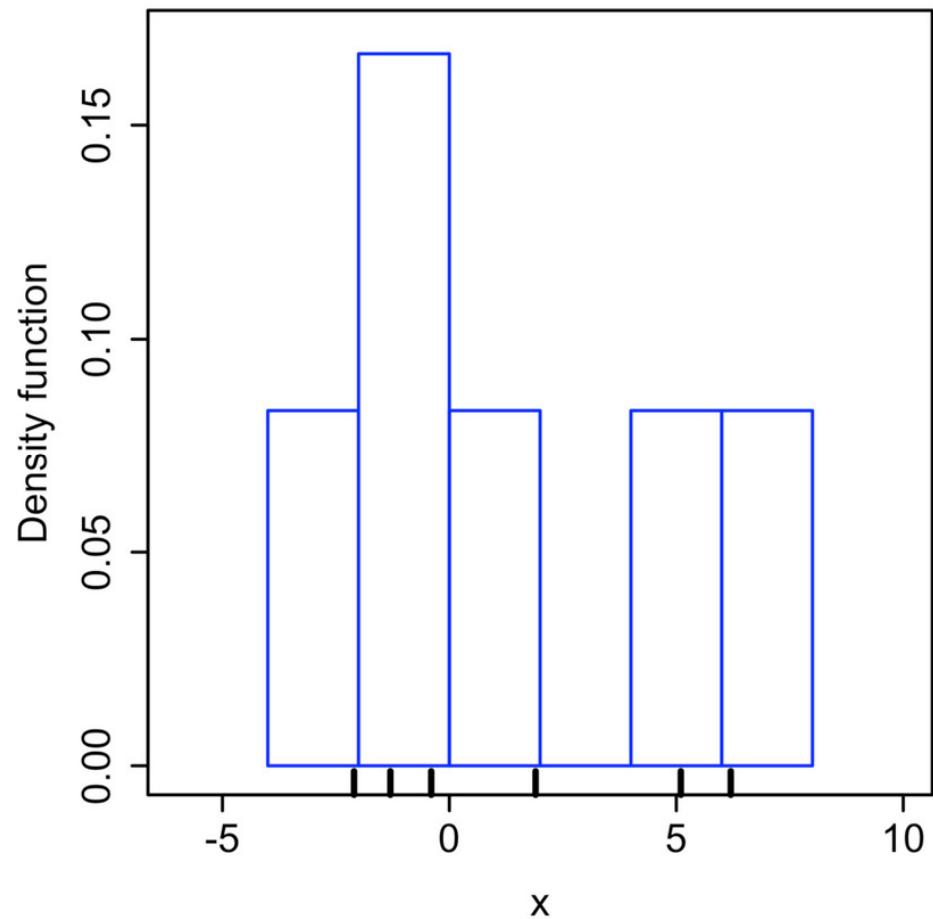


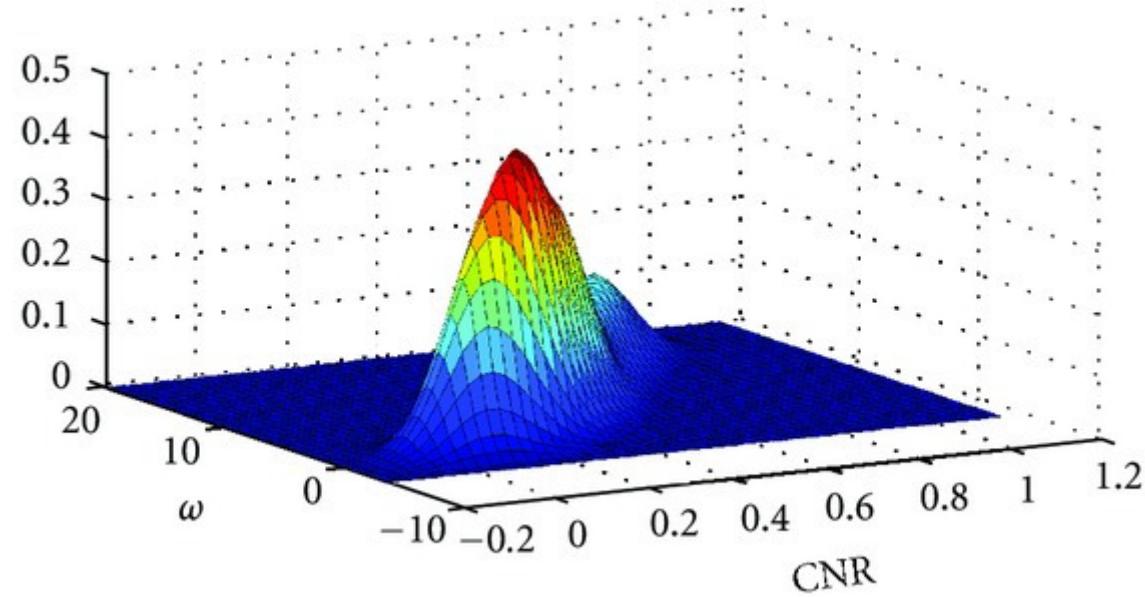
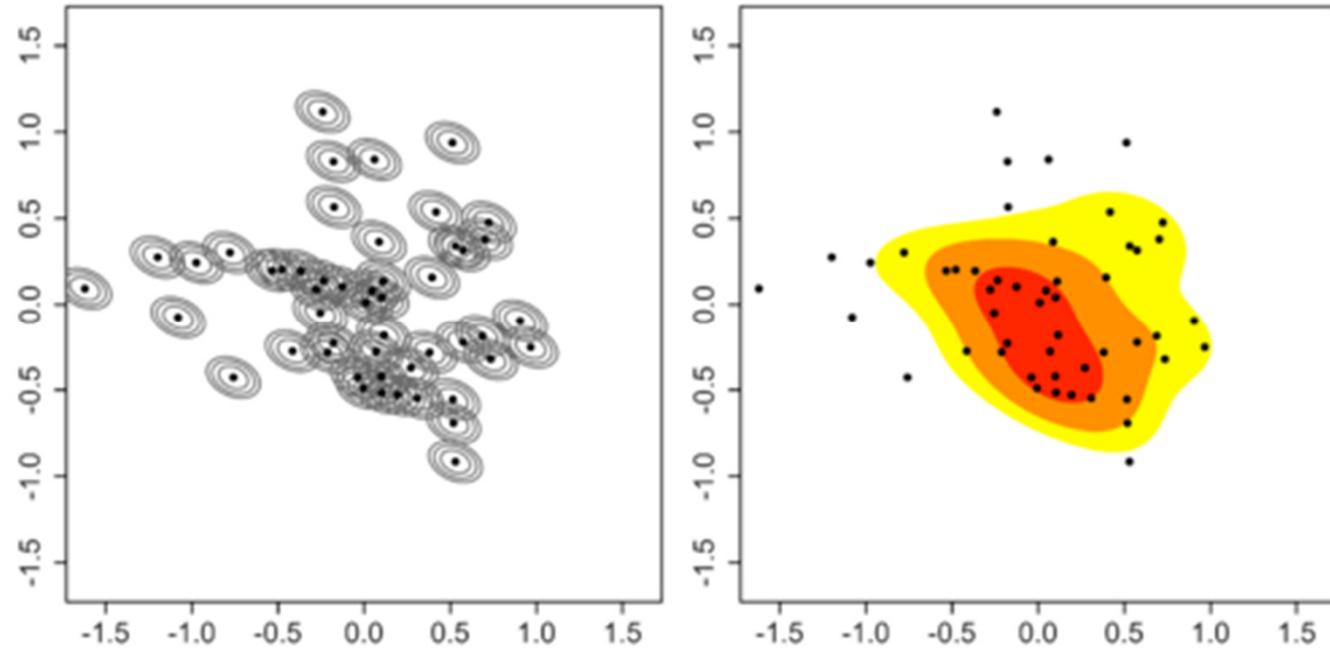
```
hrKerHref[[1]]@h  
$h  
[1] 4450.938
```

More detail?
h = 2000 m?

From movement path to space use quantification: Kernel density estimation







Estimation of bounded areas from set of random points: Theory of Set Estimation

e.g. cluster analysis, pattern recognition

Kernel density estimators, with data-based rules of
bandwidth selection:

* smoothing goes to zero as sample size goes to infinity

Provide consistent (asymptotically unbiased) estimates of the UD
(Wand and Jones 2005)

Similar convergence properties apply to estimates of bounded
areas from KDEs (e.g., Cuevas & Fraiman 1997)

despite claims otherwise (Getz et al. 2007; Getz and Wilmers 2004)

for a nice exemplification see Lichti and Swihart (2011) J. Wildl.
Manage.

Estimation of bounded areas from set of random points: Theory of Set Estimation

And how about MCPs?

MCPs will also converge as sample sizes increase provided the area one is trying to estimate is convex (Molchanov 2005).

Almost always, however, home ranges do not take simple geometric forms (Burt 1943), and MCPs typically result in Type II errors when the UD is not convex.

Therefore, the suggestion by Harris et al. (1990) to use MCPs for comparative purposes because they are “assumption-free” is misleading.

MCPs increase with sampling duration → Type I errors with datasets of short sampling duration.

Estimation of bounded areas from set of random points: But !

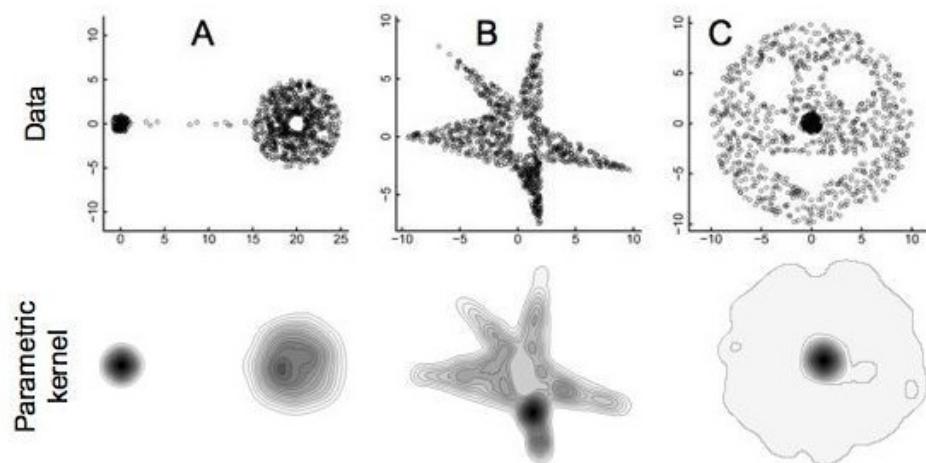
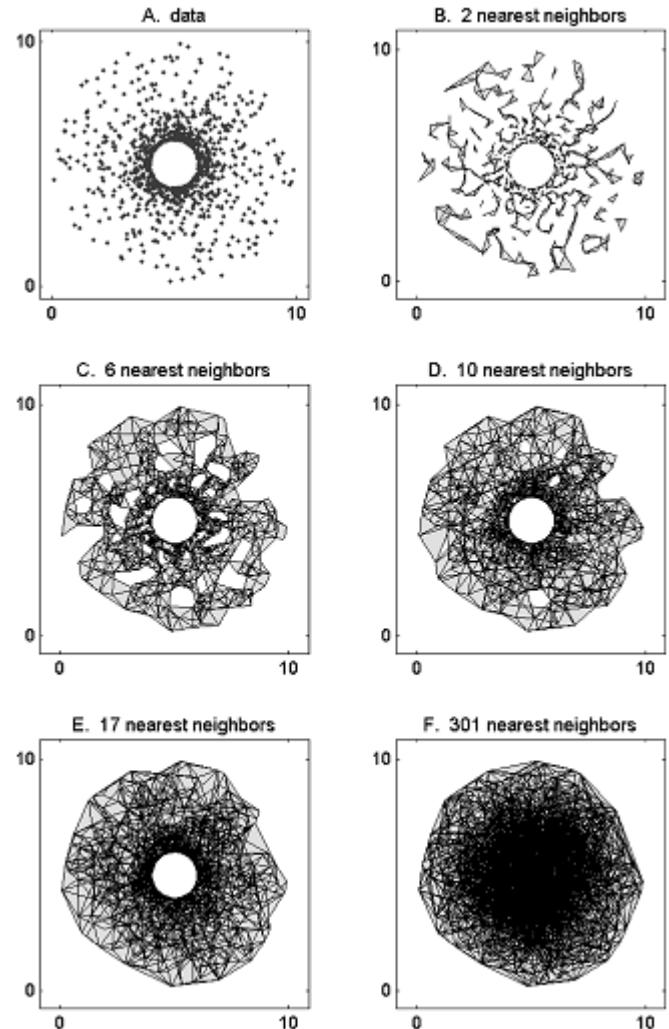
Estimates of home-range size obtained from the 95% probability contour of a KDE often decrease with sample size.

Estimates may fragment into multiple small polygons with large data sets, leaving out travel corridors between habitat patches.

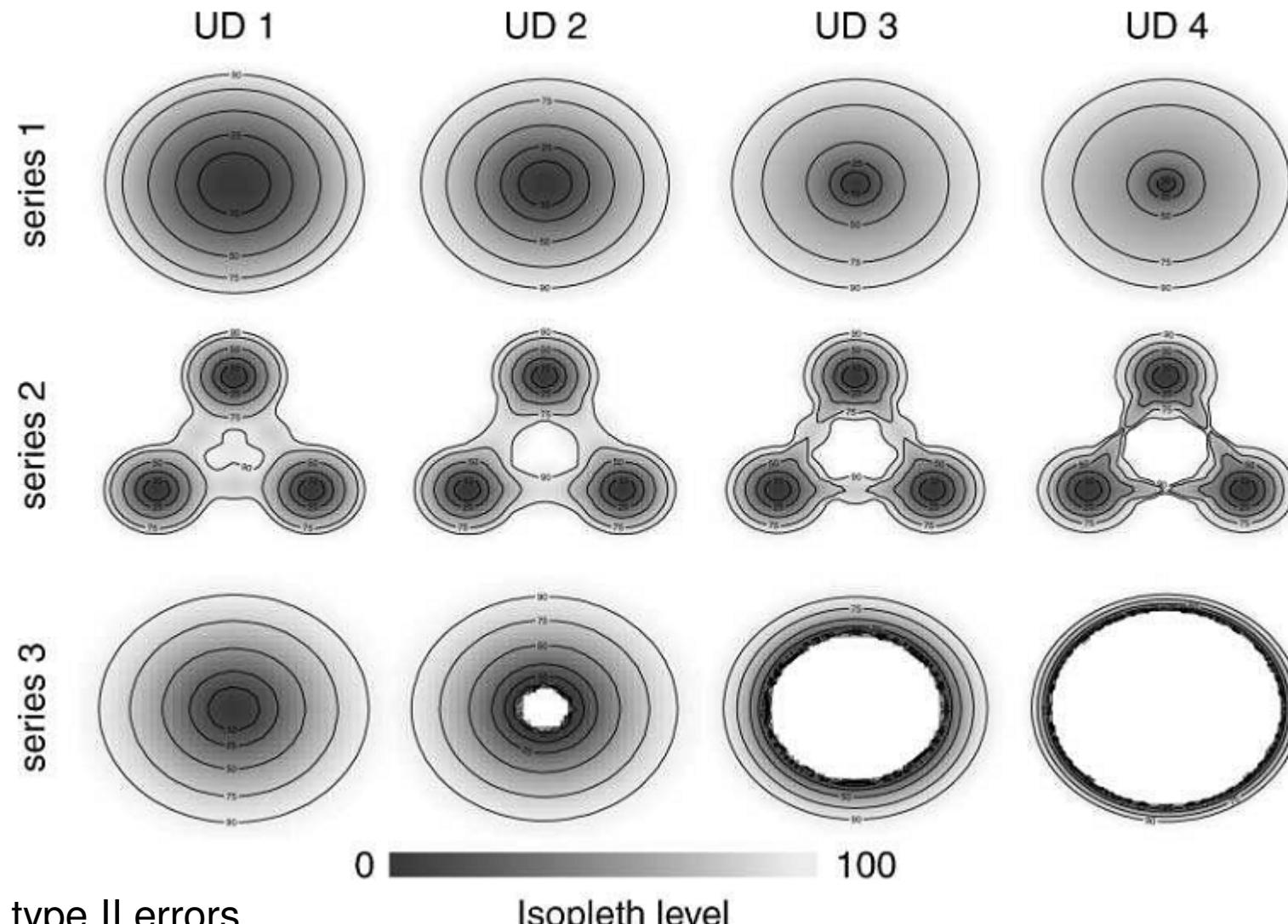
Thus, KDEs may result in Type II errors (due to oversmoothing) with small data sets and Type I errors (when restricted to a 95% contour) with large data sets.

Depending on how the estimates are ultimately used (i.e., the motivating question), the cost of these errors may or may not be large.

Estimation of bounded areas from set of random points: ‘parametric’ vs. ‘non-parametric’ kernel

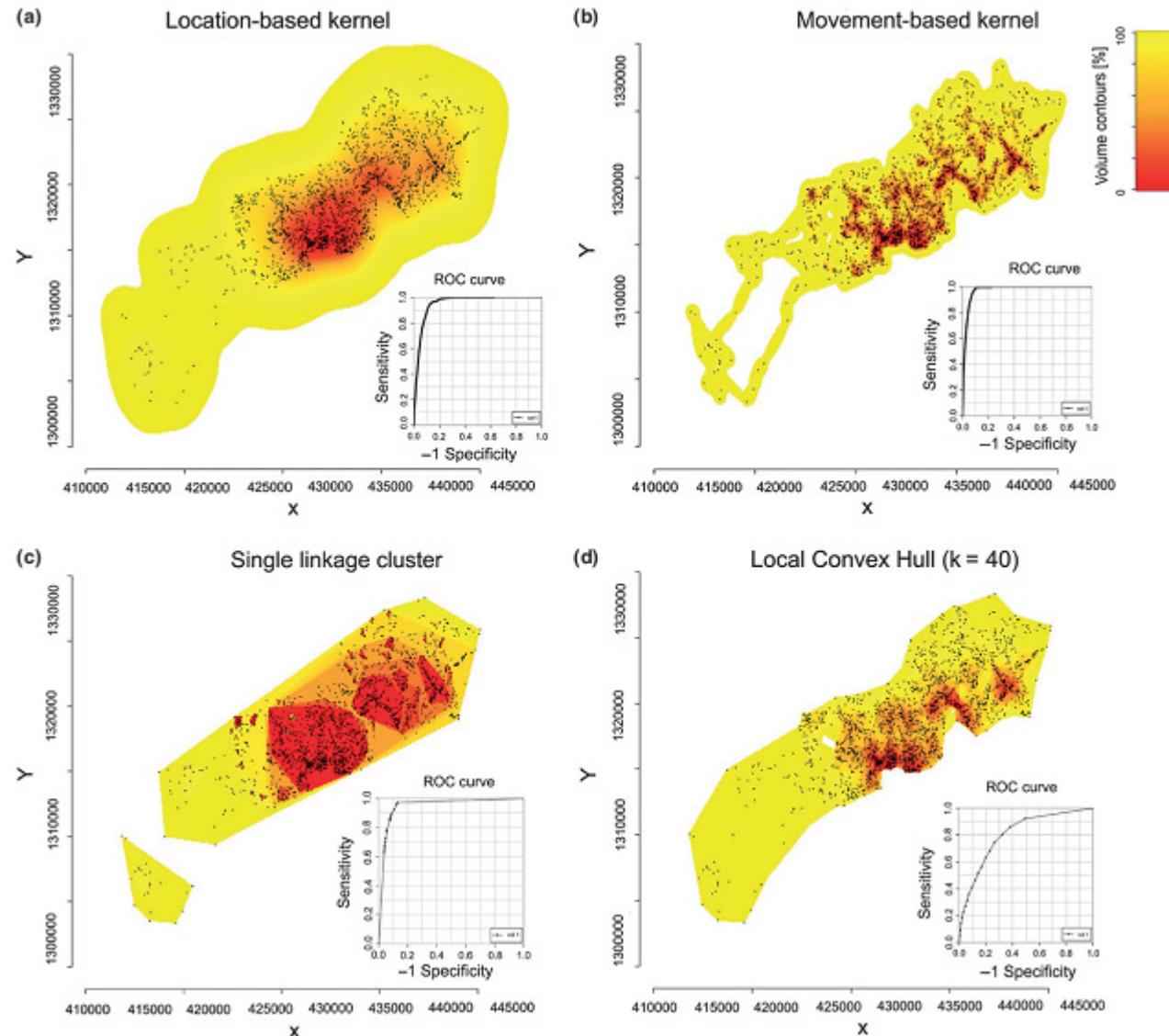


Estimation of bounded areas from set of random points: But !

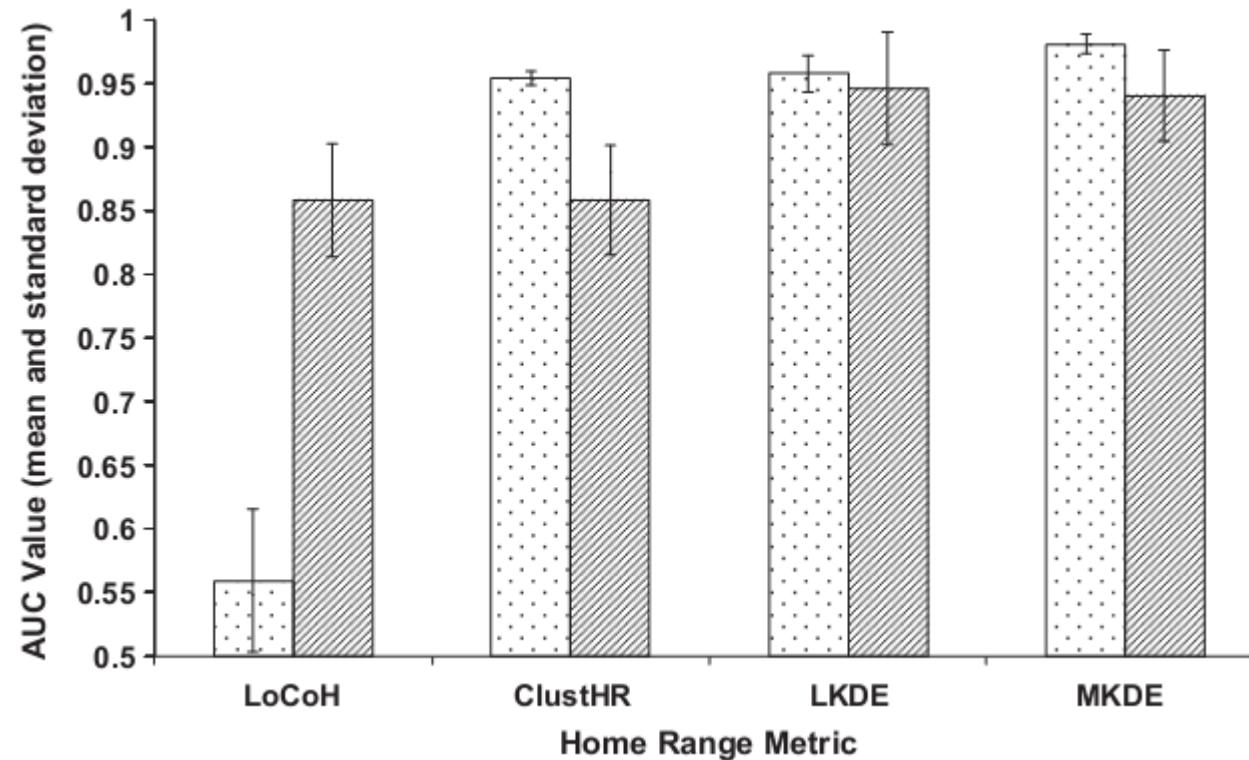


Lichti et al. 2011

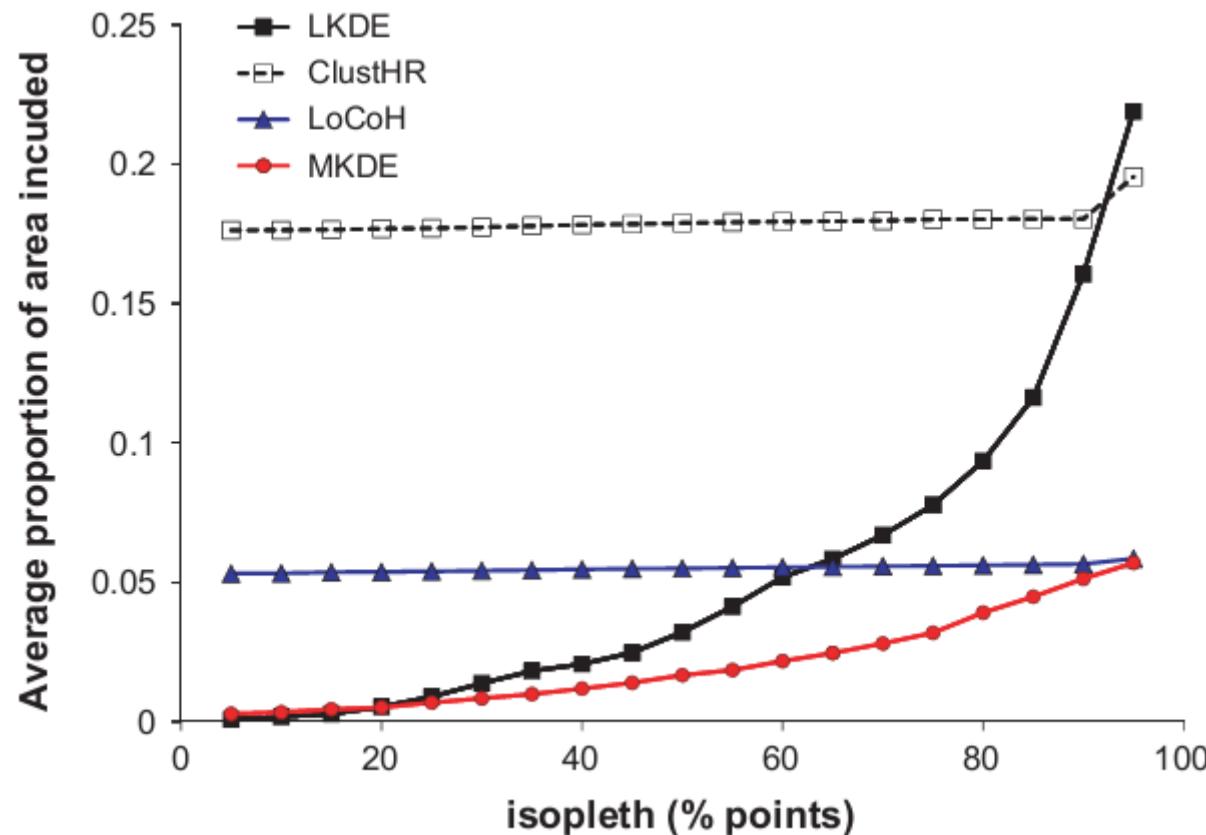
Estimation of bounded areas from set of random points: But !



Estimation of bounded areas from set of random points: But !



Estimation of bounded areas from set of random points: But !



The relatively flat area profiles of the curves for LoCoH and ClustHR reflect both their initially rapid exclusion of points and their tendency to maintain at least some isopleth area in each cluster of points as isopleth values decline.

kernel methods drop entire clusters of points at lower isopleth values, resulting in a better trade-off in error rates.

Evaluating the stationarity/site-fidelity assumption How?

Home range overlap

Multiresponse permutation procedures
(MRPP; Mielke and Berry 1982)

Mean squared displacement

Evaluating sampling design

Resampling / Variance components approach

- method, sample size, sampling regime?
- effects on statistical inference?
- contribution components sampling regime?

statistical analysis -> variance structure

Evaluating sampling design

Resampling / Variance components approach

- location data set
- simulate sampling regimes: resampling without replacement
 - estimate home ranges
- HR size ~ Subject / N sampling bouts / Timing / N fixes



Börger et al. (2006) J. Anim. Ecol.

Evaluating sampling design Resampling / Variance components approach

2001-2003: 19763 fixes, 32 roe deer (1:1 sex)

4 HR methods, 4 sampling regimes, 4 time scales

5201 fixes, 21 kestrel (18 ♂), 2 study areas

A. Village, LITS project

- i. What are the contributions of different components of the sampling regime to the total variance in home range size?
- ii. Is it sufficient to standardise the number of fixes collected to obtain unbiased statistical inference?
- iii. Which home range estimation method is the most efficient and unbiased?

Evaluating sampling design

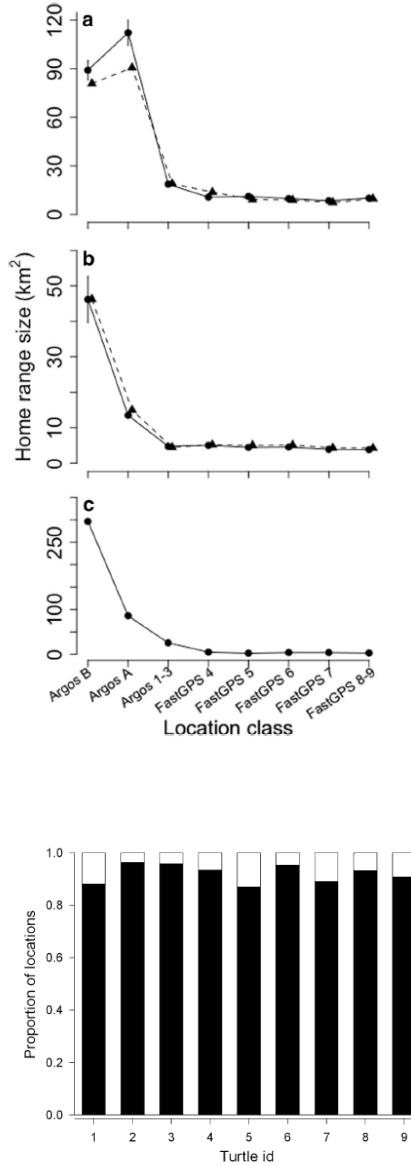
Resampling / Variance components approach

Consistent results for both species

monthly time scale	Variance components (%)				
	Subject	nDays	Timing	nFixes	Residual
MCP	25	23	-	-	51
Kernel (90%)	40	1	-	-	59

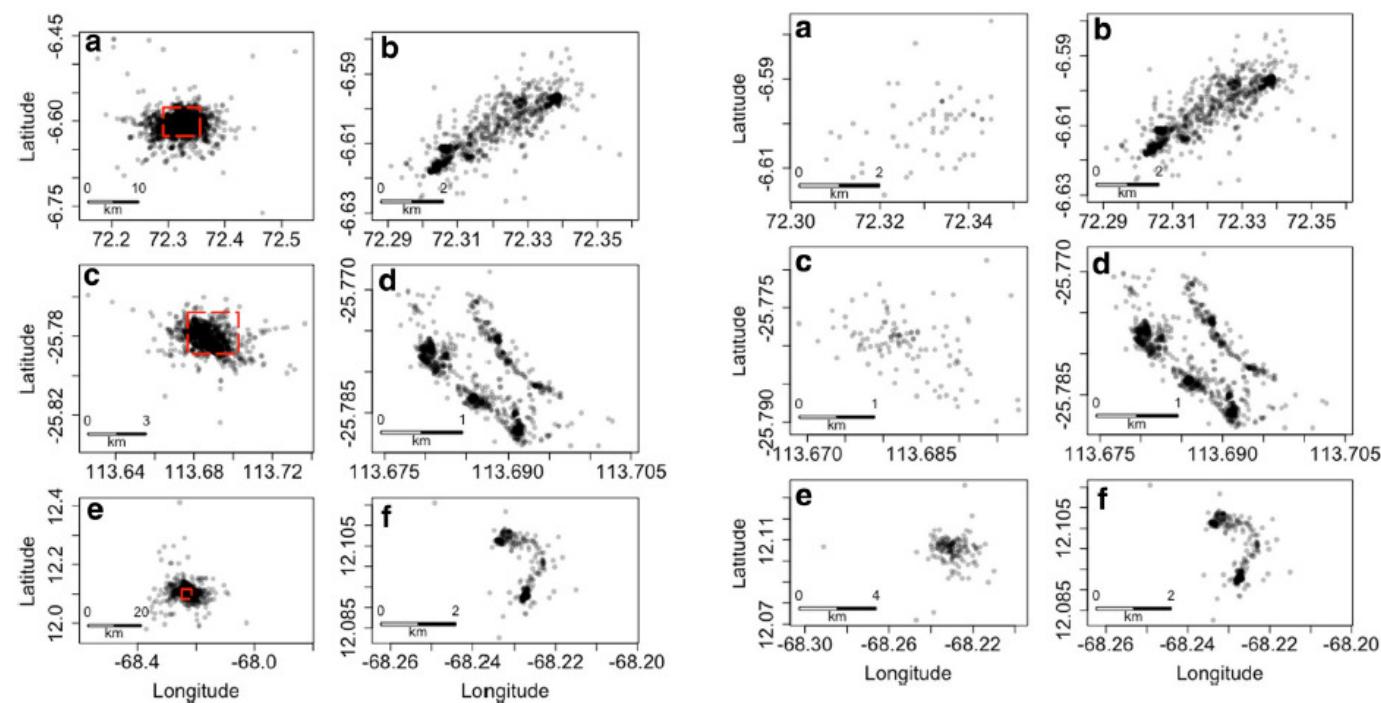
Kernel: 10 fixes/month if 90-50% isopleths

Standardising nFixes not sufficient for unbiased statistical inferences!



Implications of location accuracy and data volume for home range estimation and fine-scale movement analysis: comparing Argos and Fastloc-GPS tracking data

J. A. Thomson¹ · L. Börger² · M. J. A. Christianen^{3,4} · N. Esteban² · J.-O. Laloë¹ · G. C. Hays¹





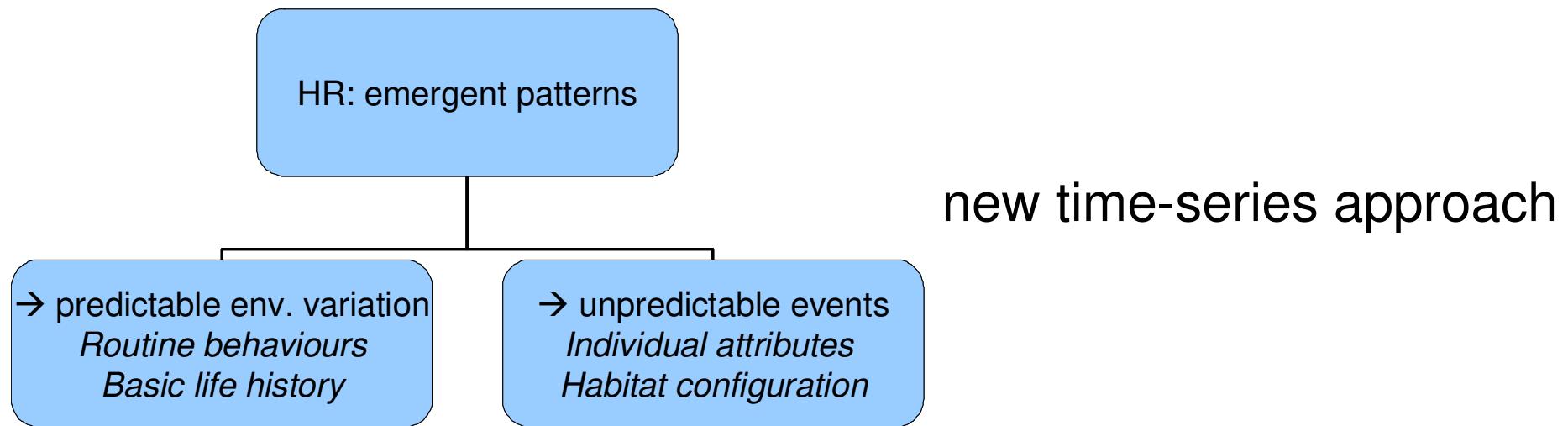
VOL. 168, NO. 4 THE AMERICAN NATURALIST OCTOBER 2006

An Integrated Approach to Identify Spatiotemporal and Individual-Level Determinants of Animal Home Range Size



Photo: R. Del Guerra

Luca Börger,^{1,2,3,*} Novella Franconi,^{3,†} Francesco Ferretti,^{3,‡} Fiora Meschi,^{3,§} Giampiero De Michele,^{3,||} Alberto Gantz,^{3,4,#} and Tim Coulson^{1,**}



HR size \sim spatial + temporal + individual + tracking error + autocorrelation



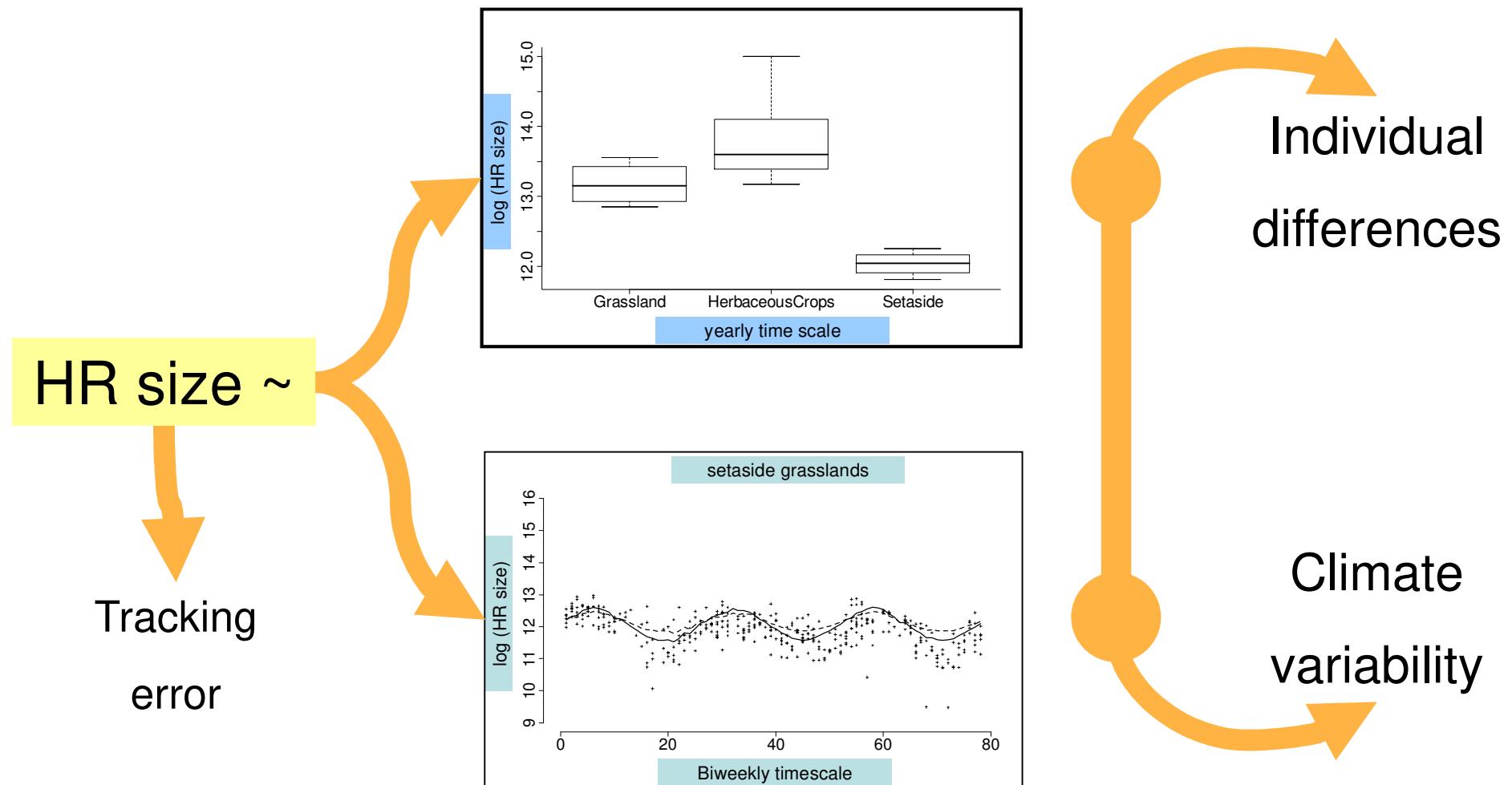
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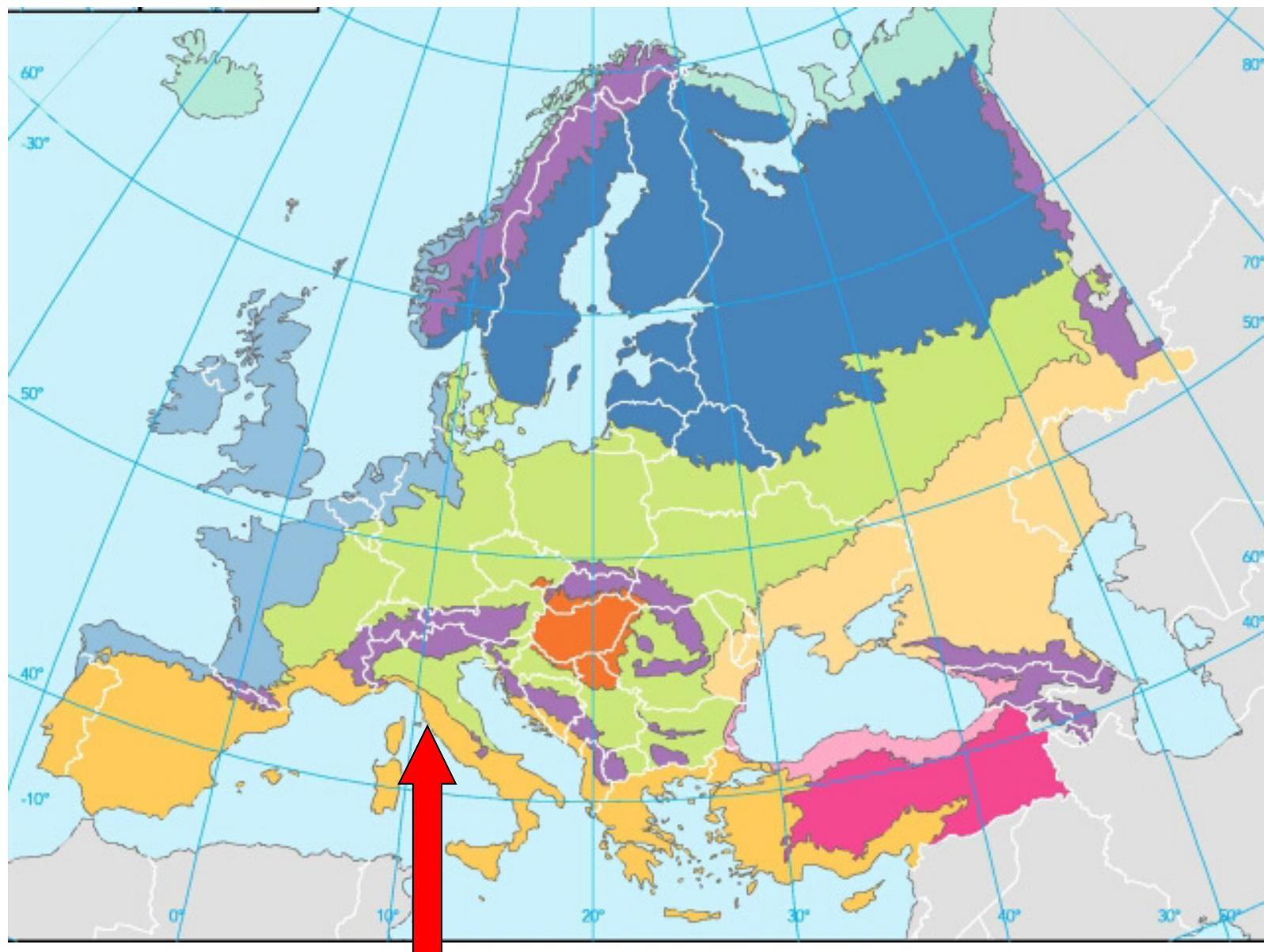


Photo: R. Del Guerra

Luca Börger,^{1,2,3,*} Novella Franconi,^{3,†} Francesco Ferretti,^{3,‡} Fiora Meschi,^{3,§} Giampiero De Michele,^{3,||} Alberto Gantz,^{3,4,#} and Tim Coulson^{1,**}



Study area



Mediterranean coastal area

Börger et al. 2006 Am. Nat.

Analysing HR data

The biogeography of animal space use

EuroDeer collaborative database

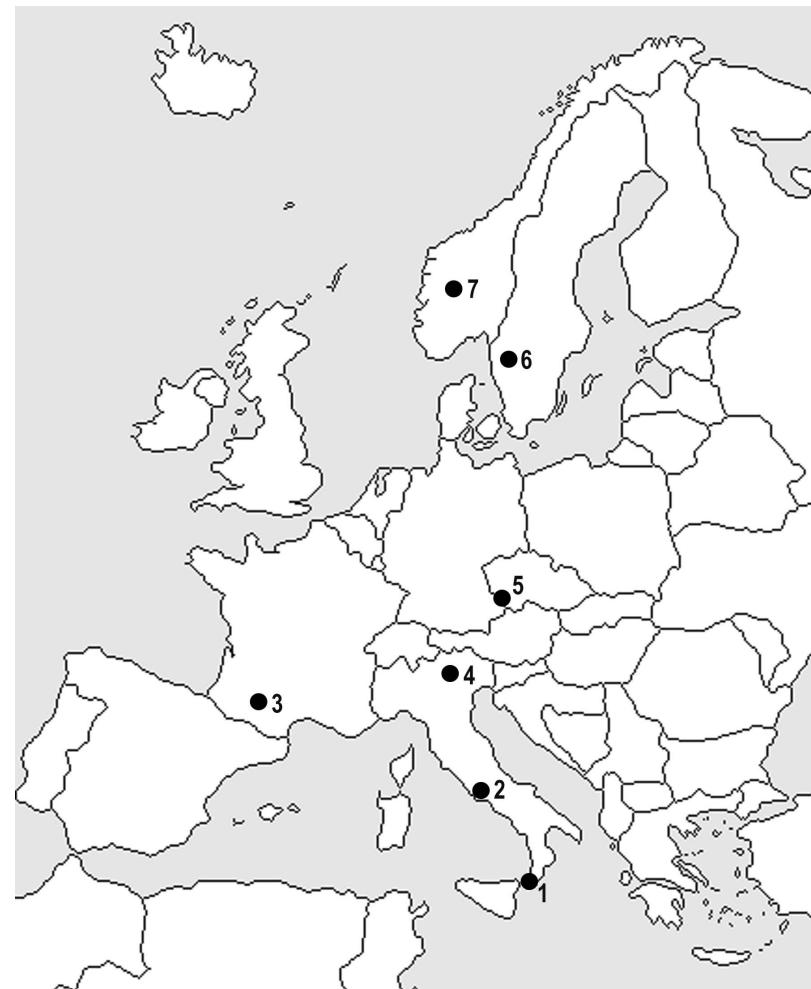
GPS data

190 female roe deer

7 areas

Weekly HR size

Mixed models



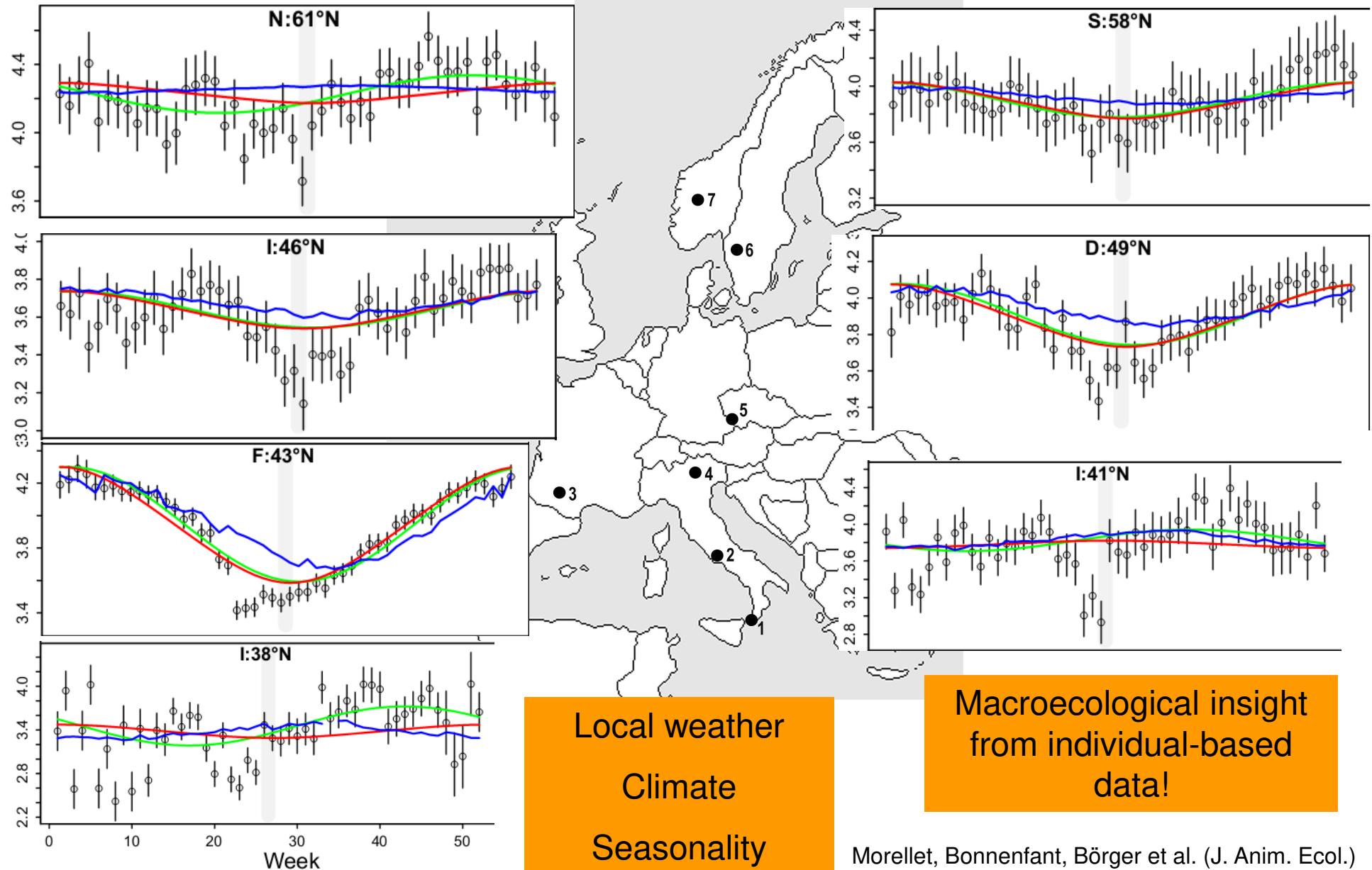
EURODEER
COLLABORATIVE
PROJECT

Sponsored by
VECTRONIC
Aerospace

Morellet, Bonnenfant, Börger et al. (J. Anim. Ecol. accepted)

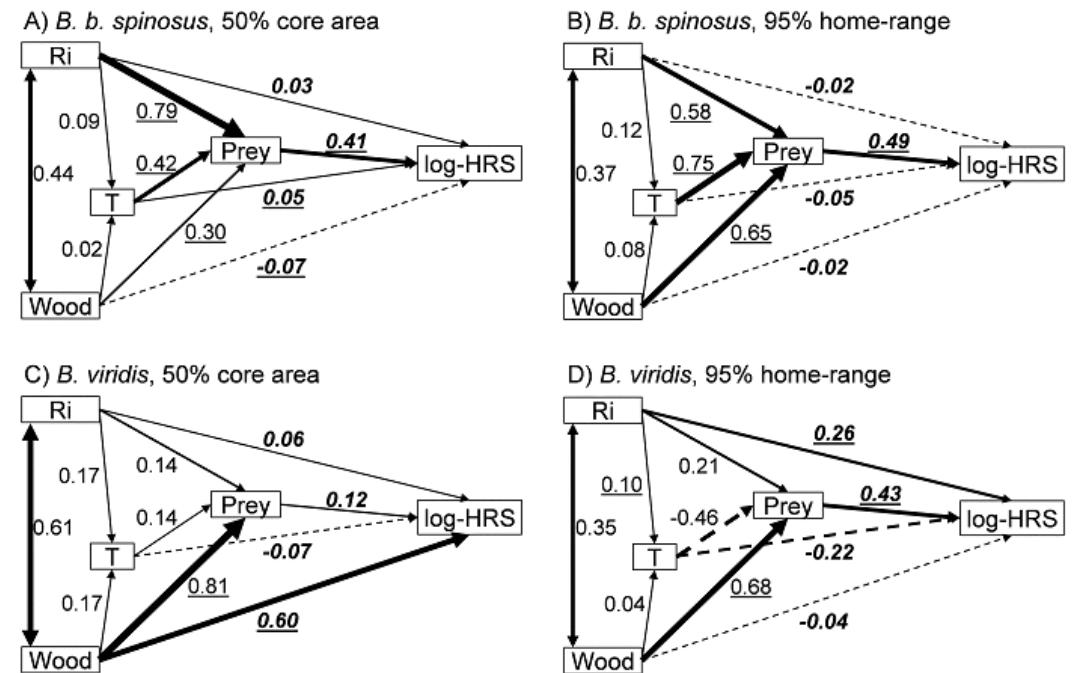
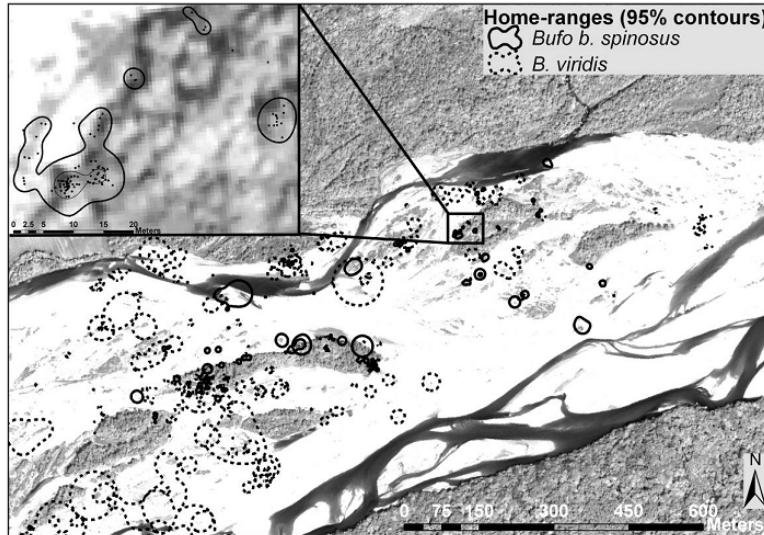
Analysing HR data

The biogeography of animal space use



Behaviour-based HR data

The biogeography of animal space use



Summer HR size of 2 amphibian species:
 50% (resting) & 95% (foraging) areas
 → Habitat structure (complexity): direct effect
 → prey density
 → between-species differential space use:
 coexistence!

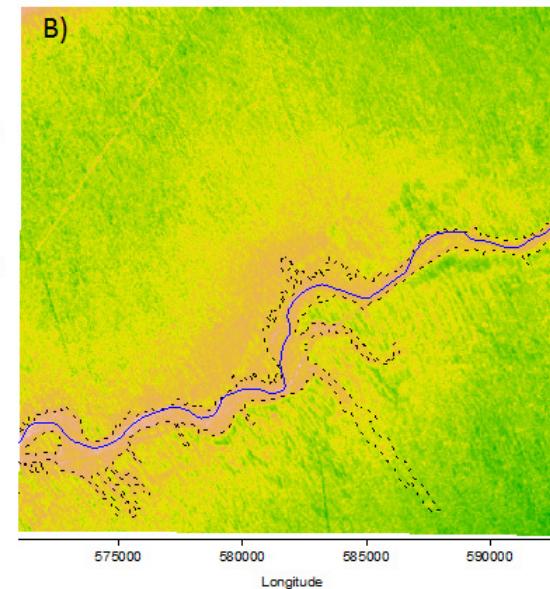
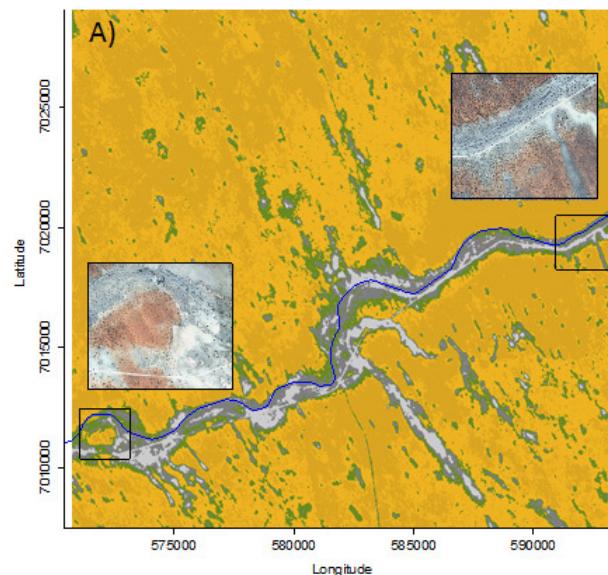
Socially informed dispersal in a territorial cooperative breeder

(in press – J. Anim. Ecol.)

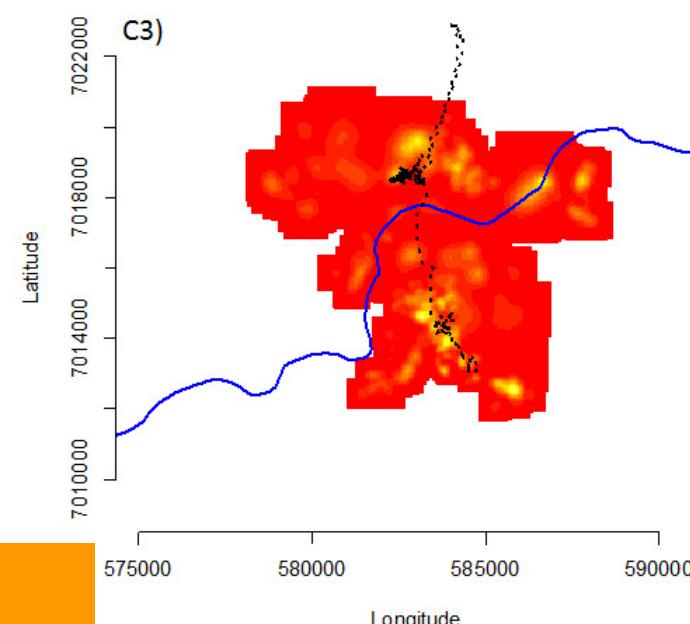
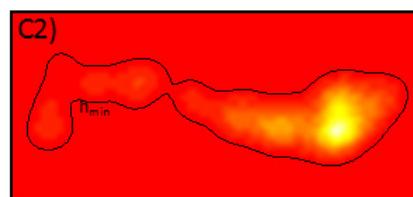
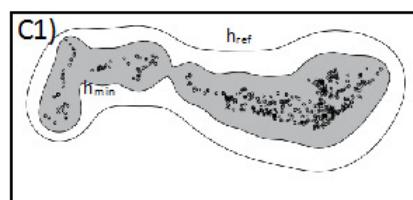
Gabriele Cozzi^{1,2,*}, Nino Maag^{1,2}, Luca Börger³, Tim Clutton-Brock^{2,4}, Arpat Ozgul^{1,2}

Aims: Investigate the effect of the social landscape on movement behaviour and decision making during the transient phase of dispersal in a socially and spatially structured species (meerkats).





Environmental layers
Satellite habitat map +
DEM



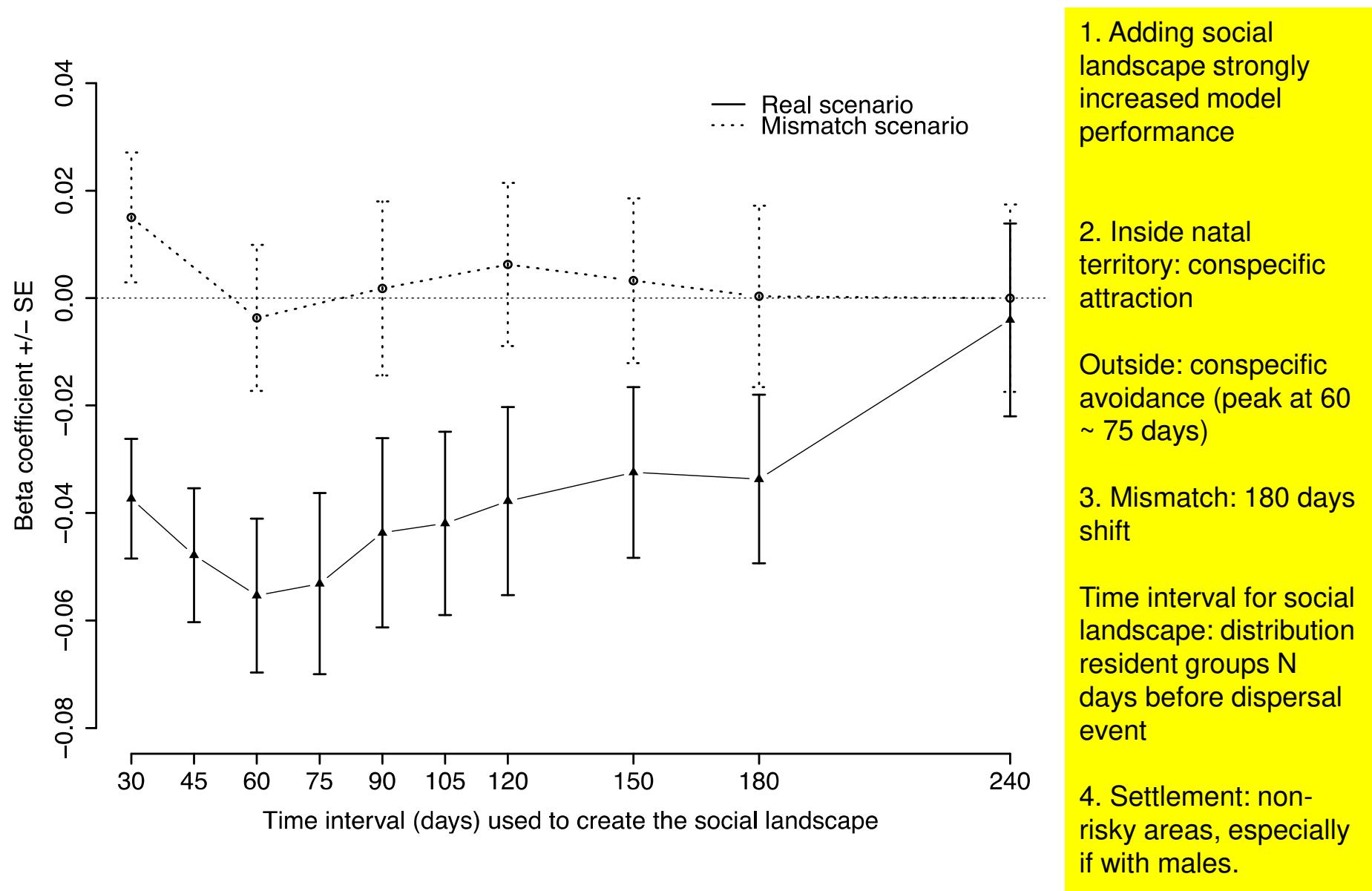
GPS collars (dispersers –
47 coalitions; 12 settled)

Observations:
coalition size; sex

Step selection functions

Social landscape (resident)
 Σ KUD (resident) * group size

Dispersing coalitions step selection coefficients associated with the distribution of resident groups.



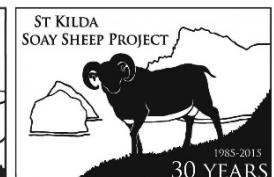
Declining home range area predicts reduced late-life survival in two wild ungulate populations



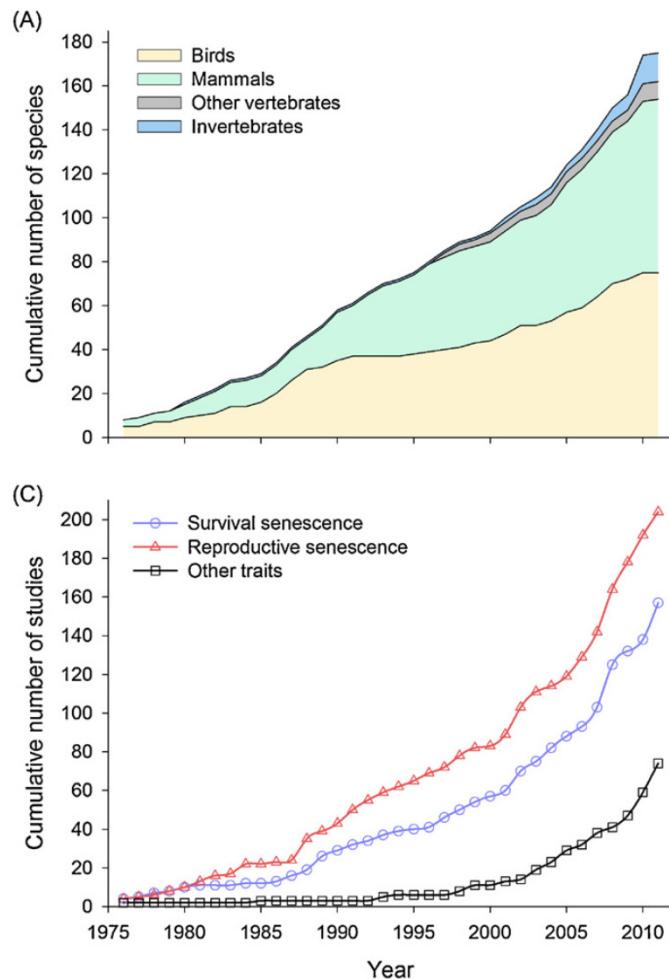
Hannah Froy, Luca Börger, Charlotte E Regan, Alison Morris, Sean Morris , Jill G Pilkington, Michael J Crawley, Tim H Clutton-Brock, Josephine M Pemberton & Daniel H Nussey



THE UNIVERSITY
of EDINBURGH



Age-related variation in behaviour



Demographic senescence
is increasingly documented

Other traits less clear

Behaviour is highly variable

Within and between individuals

Humans, domestic
lab animals



Declines in activity levels, visual
acuity, muscular function, athletic
ability

Longitudinal field studies

Soay sheep on St Kilda

Since 1985

Red deer on the Isle of Rum

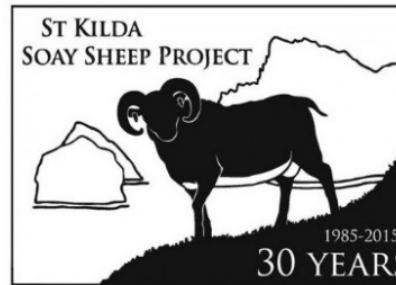
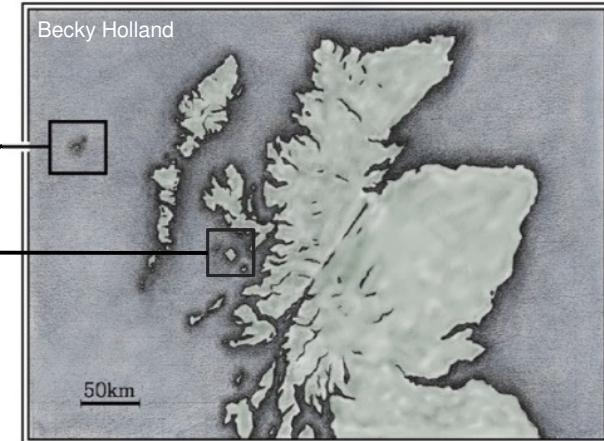
Since 1972

Individuals marked at birth

Lifelong data on repro, survival, phenology, morphology, physiology

Demographic senescence evident

Sex-specific patterns



Estimating home ranges

30 – 40 annual censuses

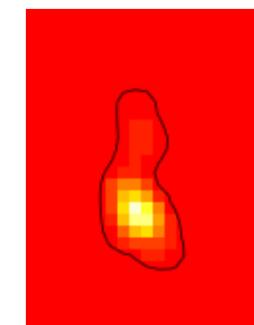
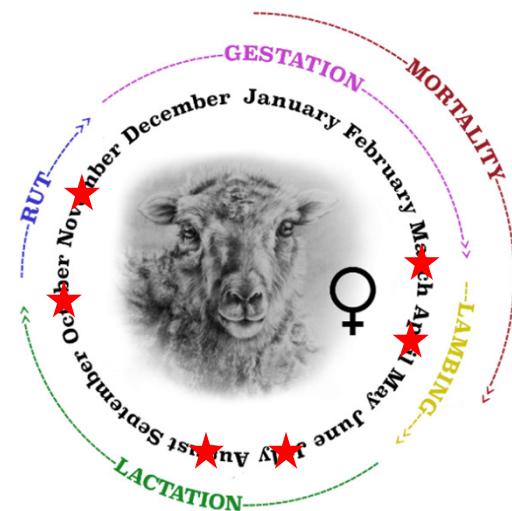
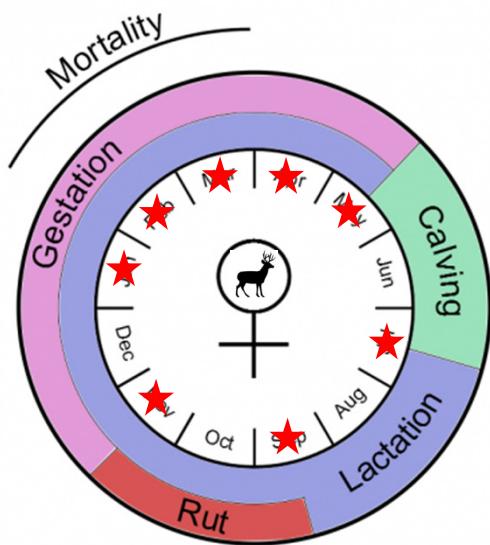
Individual locations to nearest 100m

Home ranges estimated using kernel density methods in *adehabitatHR*

Ad hoc method, 70% isopleth

Annual home range size and quality

Regan et al 2016 Ecology Letters



Froy et al. (Ecology Letters, accepted)

Estimating home ranges

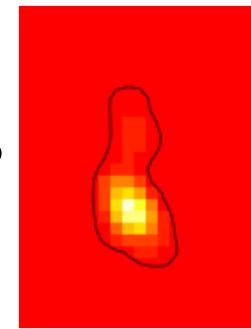
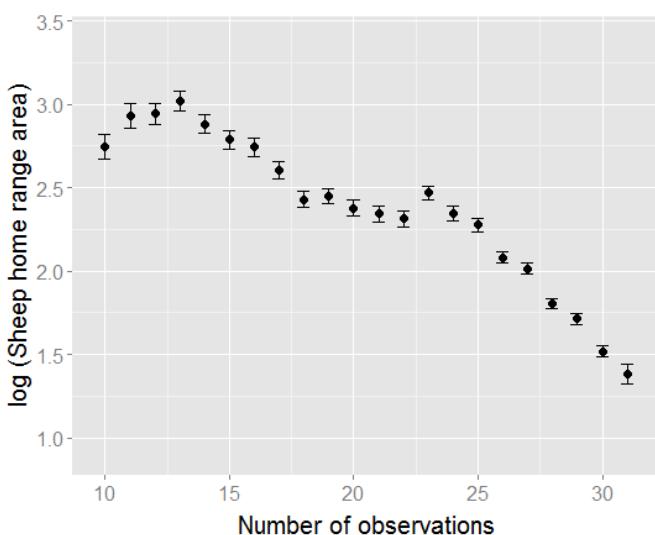
30 – 40 annual censuses

Individual locations to nearest 100m

Home ranges estimated using kernel density methods in *adehabitatHR*

Ad hoc method, 70% isopleth

→ Subsample data to control for variation in number of observations



Examining age effects

Within-individual age effects

$$\text{Age} + \text{Age}^2$$

Between-individual effects

$$\text{Longevity} + \text{Longevity}^2$$

Abrupt terminal shifts

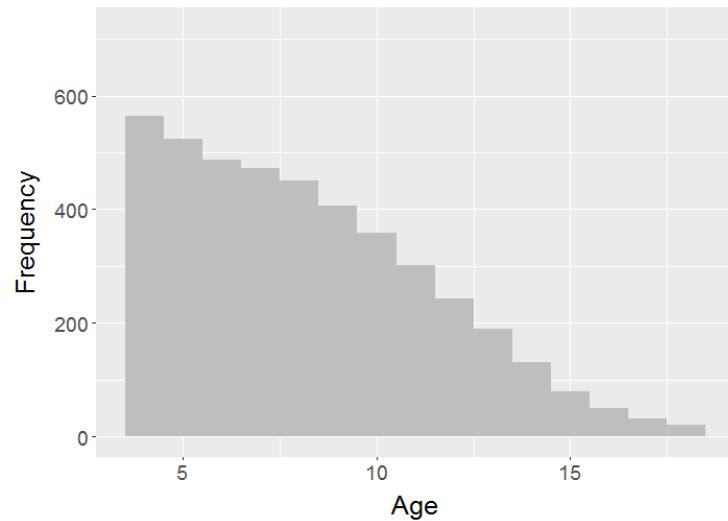
Final year

Additional fixed effects

Had calf (female deer); Trips sampled (sheep); HR size (sheep HR quality)

Random effects

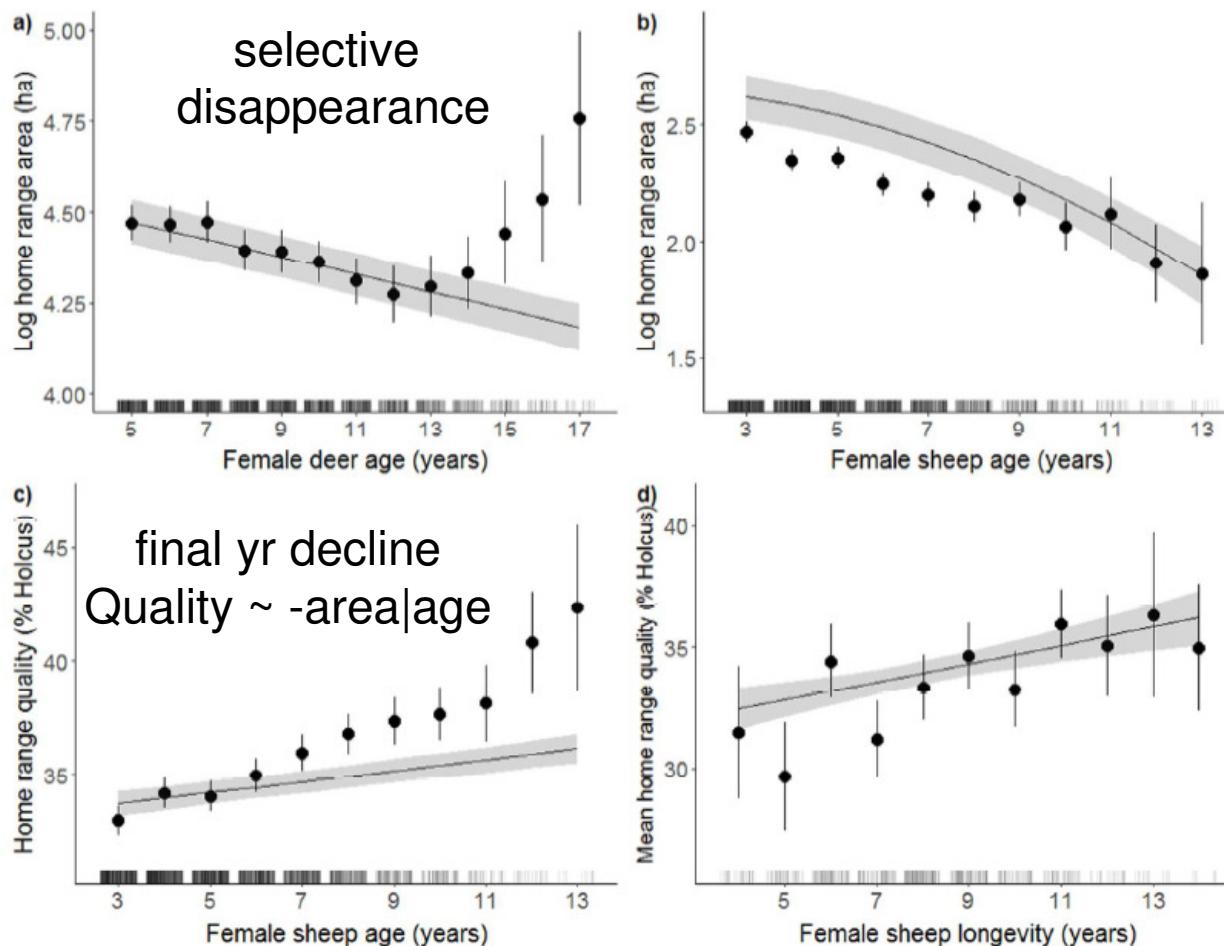
Individual + Year



Froy et al. (Ecology Letters, accepted)

This resulted in 2555 estimates of annual home range area for 377 female deer, and 2226 estimates for 535 female sheep (mean 6.8 and 4.2 observations per individual, respectively). The mean annual core home range area was 132.20 ± 156.54 SD hectares for female red deer, and 14.84 ± 14.67 for Soay sheep.

Figure 1. Relationships between female age and home range area in a) red deer ($n=2555$ observations of 377 females) and b) Soay sheep ($n=2226$ of 535 females); c) female home range quality and female age; and d) female longevity and mean home range quality in Soay sheep. Points and bars show raw data means and associated standard errors. Black lines show predictions of best model with standard errors around this prediction in grey shading (see Table 1). Rug plots on the inside of the x-axes show the distribution of the raw data.

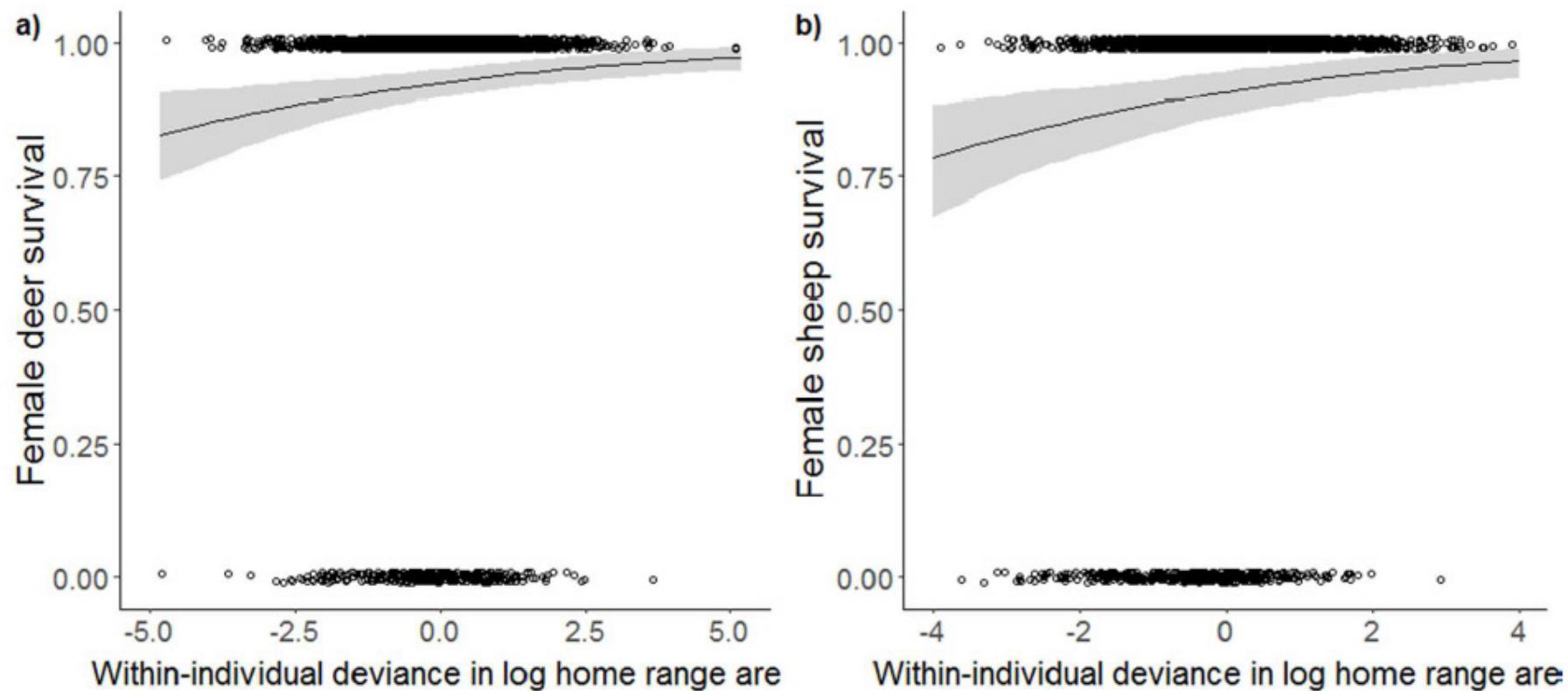


no evidence for a terminal shift in home range area In both systems

Repeatability of home range area for individual females over their lifetime was 0.747 (CI=0.712-0.777) for deer and 0.509 (CI=0.438-0.583) for Sheep

individual repeatability of sheep home range quality was 0.842 (CI=0.820-0.861).

Figure 2. Relationships between within-individual deviance in home range area and female survival in the subsequent year in a) red deer (n=3315 observations of 490 females) and b) Soay sheep (n=3158 of 725 females). Points show jittered raw data; black lines show model predictions and associated 95% confidence intervals in grey shading (see Table 2a & 2d).



within-individual declines in home range size were associated with reduced
subsequent winter survival probability

Froy et al. (in review)

Question-driven approach to HR studies: The road to success

1. Define precise research questions
2. Identify spatio-temporal scales and units of analysis
3. Select space-use metrics and covariates to test specific research hypotheses
4. Define sampling design and inferential approach
5. Assess the strength of conclusions
6. Archive data

Dynamic Approach to Space and Habitat Use Based on Biased Random Bridges

Simon Benhamou*

CEFE, CNRS, Montpellier, France

Trade-off between Brownian motion (too simplistic) and Biased CRWs (too complex) for functional bridges

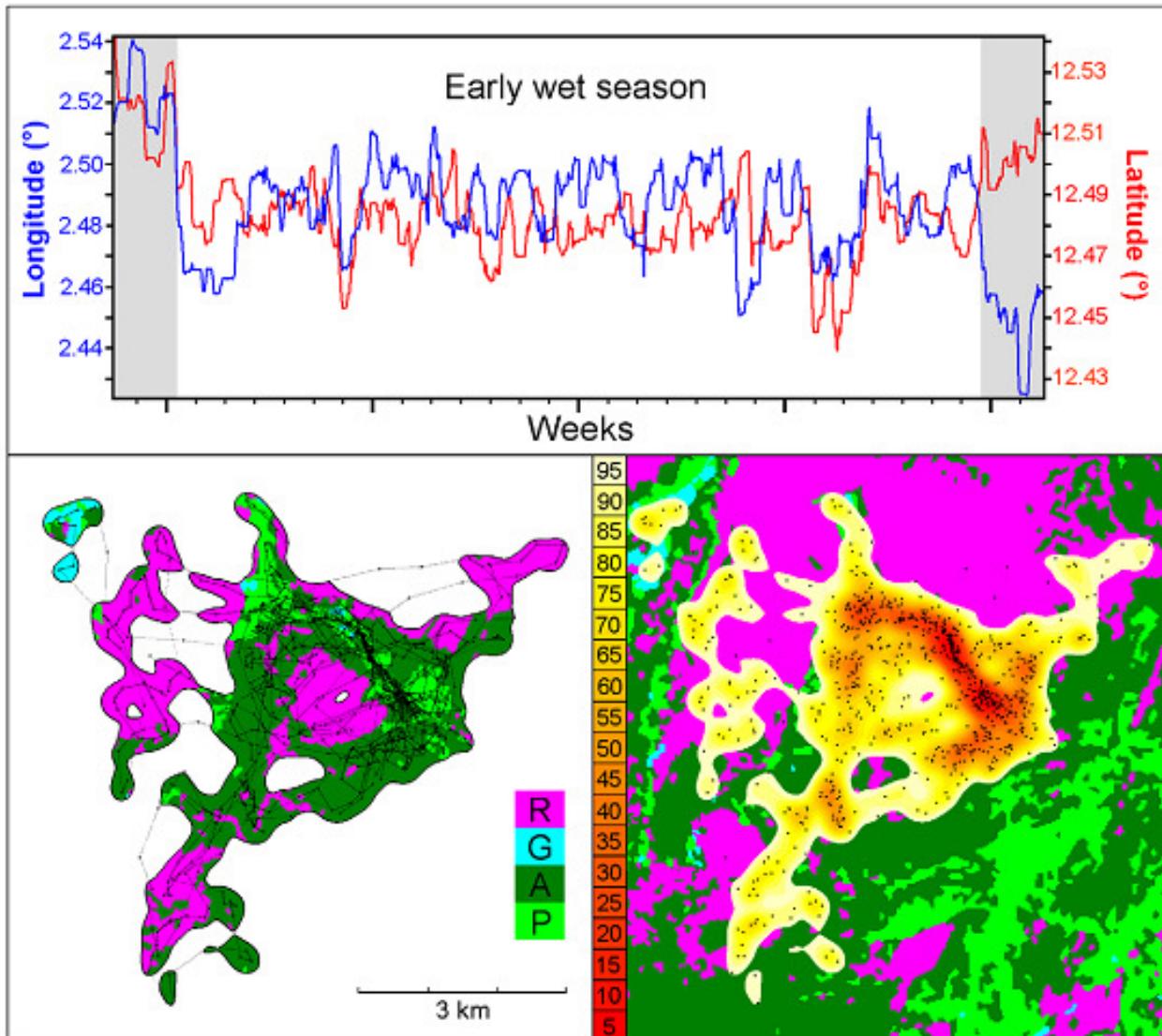
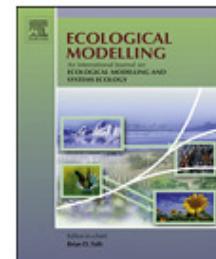


Figure 1. Utilization Distribution (UD) of an African buffalo herd for a 4-week stationary period computed using simplified BRBs ($\sigma_{min} = 100$ m, $D = 440$ m²/min and $T_{max} > 30$ min) through the MKDE method ($h_{min} = \sigma_{min}$ and $h_{max} = (\sigma_{min}^2 + DT_{max}/2)^{0.5}$). The top panel shows how the period considered (early wet season, indicated by the white background) was delineated by marked and durable changes in mean or variance of longitude or latitude (computed over a few days in a sliding window). The bottom left panel shows the herd movement (big dots represent GPS relocations recorded at 30-min intervals and tiny dots locations interpolated along track segments at 1-min activity intervals) and the different habitat types available within 95% UD cumulative frequency isopleths (R: Rocky grounds, G: Forest galleries, P: Perennial grasses, A: Annual grasses). The bottom right panel shows the GPS relocations (black dots) and UD cumulative frequencies up to 95% (the colour attributed to a given percentage p applies to areas comprised between p and $p-5\%$ isopleths).



Short communication

Beyond the Utilization Distribution: Identifying home range areas that are intensively exploited or repeatedly visited

Simon Benhamou*, Louise Riotte-Lambert

Centre d'Écologie Fonctionnelle et Évolutive, CNRS, Montpellier, France

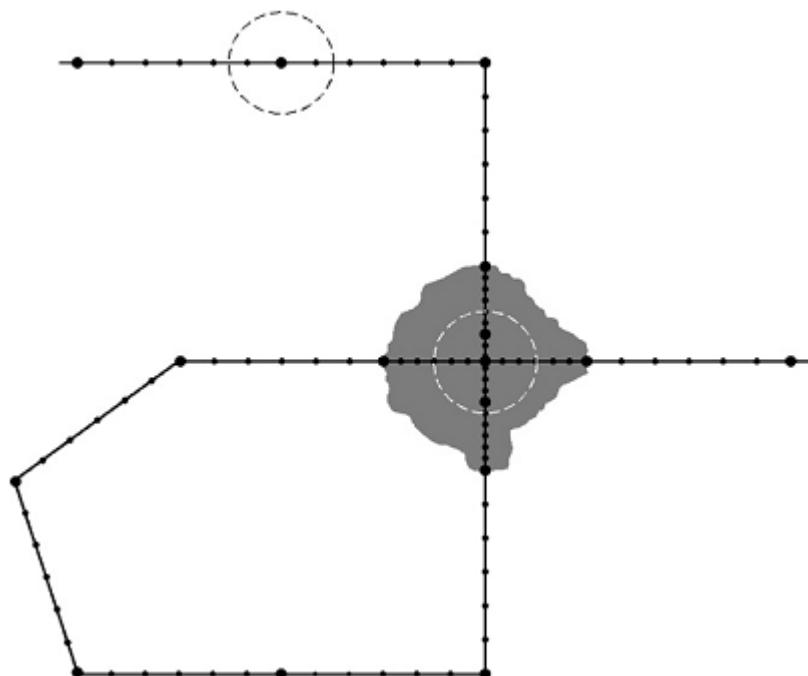


Fig. 1. Idealized movement example. The animal is assumed to move at a constant speed, except when entering the gray area. The animal visits this particular area twice, and adopts a reduced speed to exploit it more intensively, two times lower than its current speed on one occurrence, and three times lower on the other. Big dots correspond to locations recorded every 30 min, and small dots to in-between locations interpolated at 5-min intervals. The virtual circle used to compute the residence time and the number of visits is represented twice: one time centered on a location outside the gray area (drawn in black), and one time centered on the crossing point at the heart of the gray area (drawn in white). In analyses of actual data, it will be centered successively on every (interpolated or recorded) location.

ID: Intensity Distribution

(spatial distribution mean residence time per visit)

RD: Recursion Distribution

(spatial distribution number of visits)

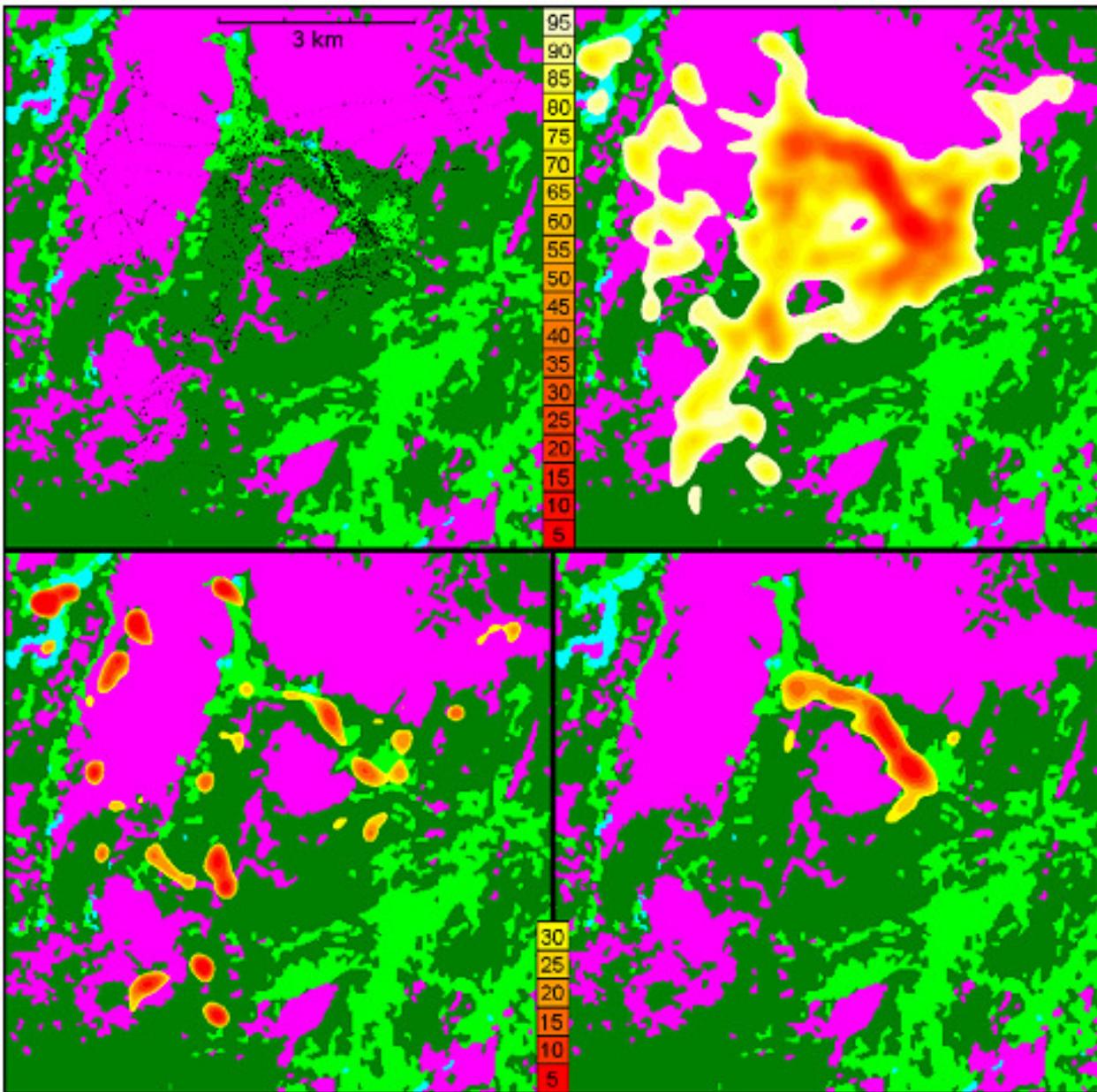


Fig. 2. Movement (top left panel), UD (top right panel), ID (bottom left panel) and RD (bottom right panel) of an African buffalo herd for a 4-week stationary period in early wet season of 2008. GPS locations were recorded at 30-min interval, and interpolated at 5-min activity time intervals (big and small dots, respectively, in the top left panel). These three distributions were computed with the weighted MKDE method. The UD is drawn up to 95% cumulative frequencies (the color attributed to a given percentage p applies to areas comprised between p and $p-5\%$ isopleths). As the ID and RD are computed with the only purpose to identify high density areas, these two latter distributions are drawn only up to 30% cumulative frequencies, with a stretched color code for better visibility. Four habitat types are represented: "Rocky grounds" (magenta), "Forest galleries" (cyan), "Perennial grasses" (light green), and "Annual grasses" (dark green). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)



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Periodicity analysis of movement recursions

Louise Riotte-Lambert*, Simon Benhamou, Simon Chamaillé-Jammes

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HIGHLIGHTS

- ▶ Understanding recursion patterns is key to understand animal movements.
 - ▶ We present an approach to study the periodicity of recursions.
 - ▶ The approach is based on Fourier and wavelet analyses.
 - ▶ Several periodic patterns are revealed in an example with real-world data.
-

How often is a given area within a home range revisited?

To what extent are revisits regularly spaced in time?

Daily movements → home range patterns

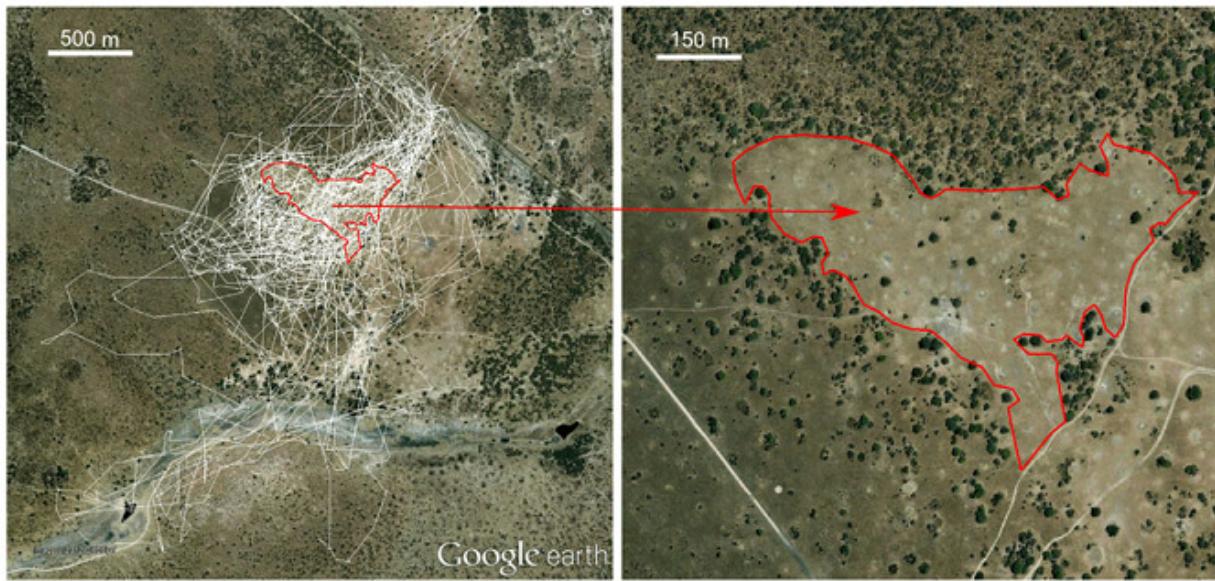


Fig. 1. Movement of the studied impala between the 16th of August and the 14th of November 2009 (white line, left panel). The area of interest on which we focused is the open area delimited by a solid red line (right panel). Background: Google Earth® (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

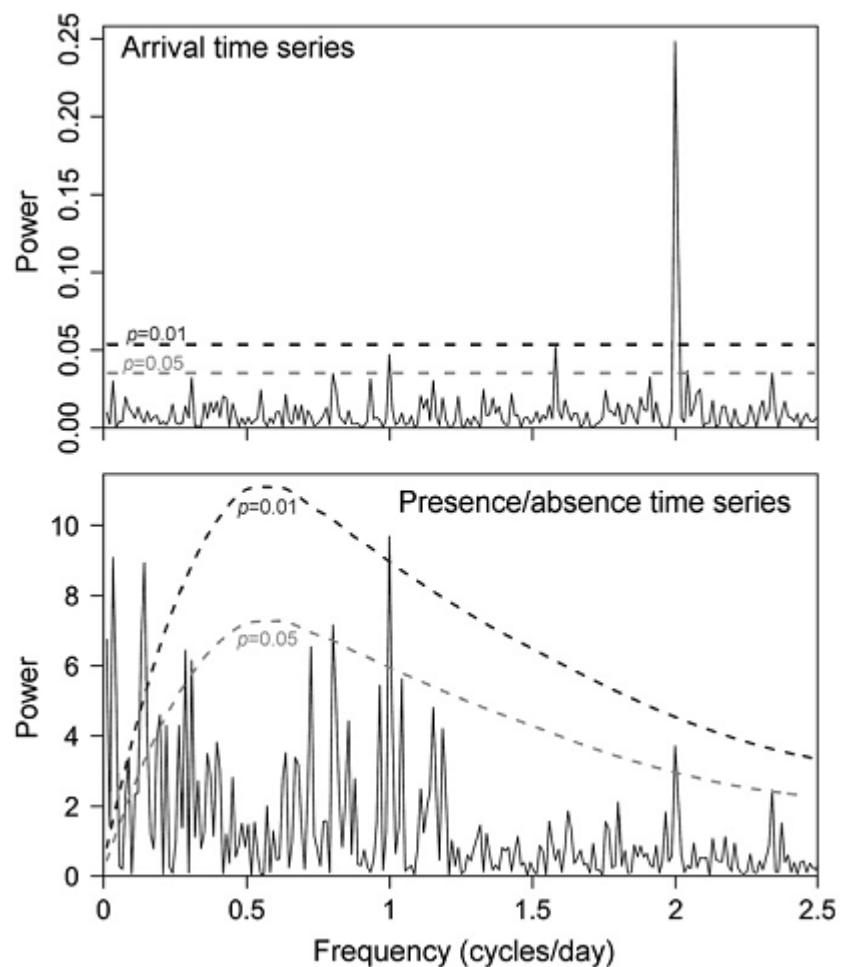
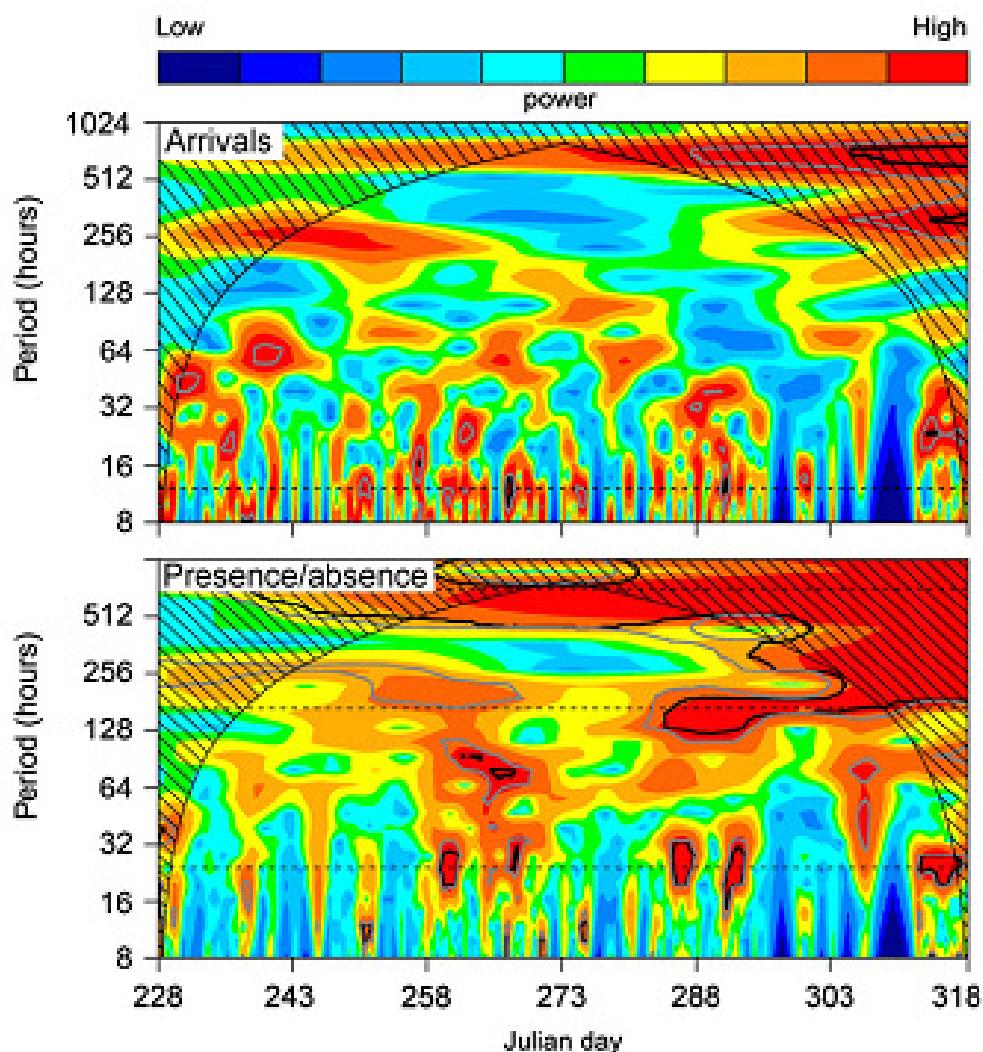
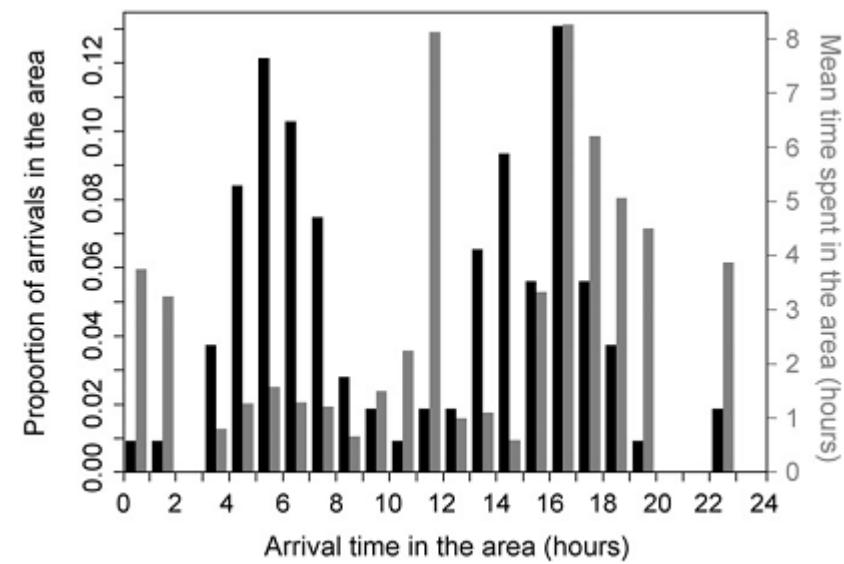
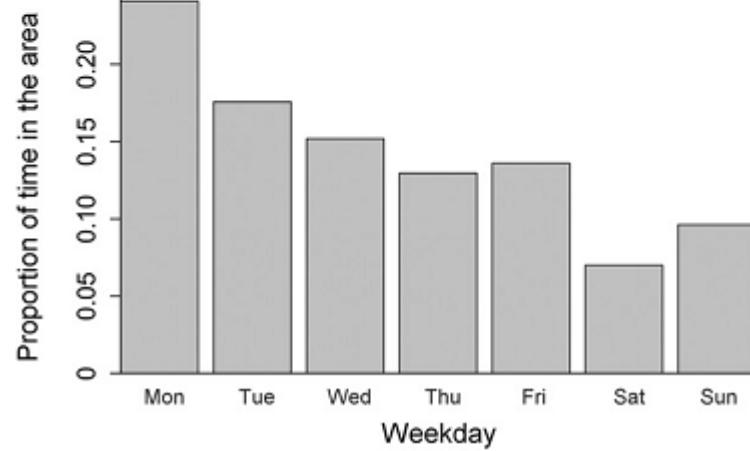
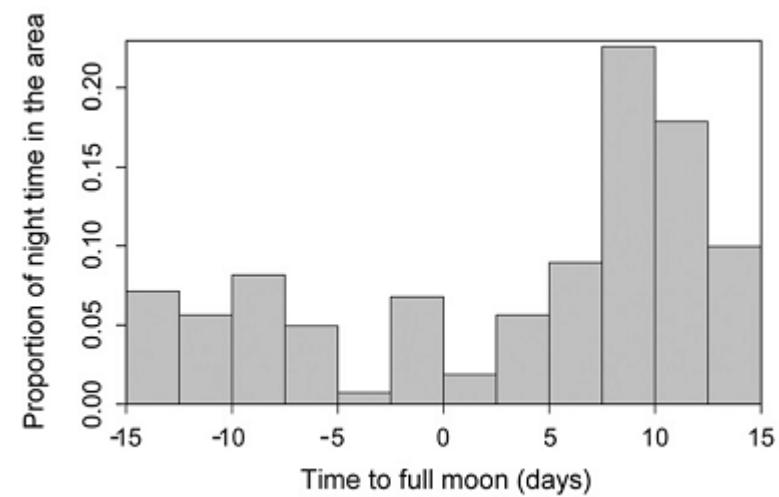
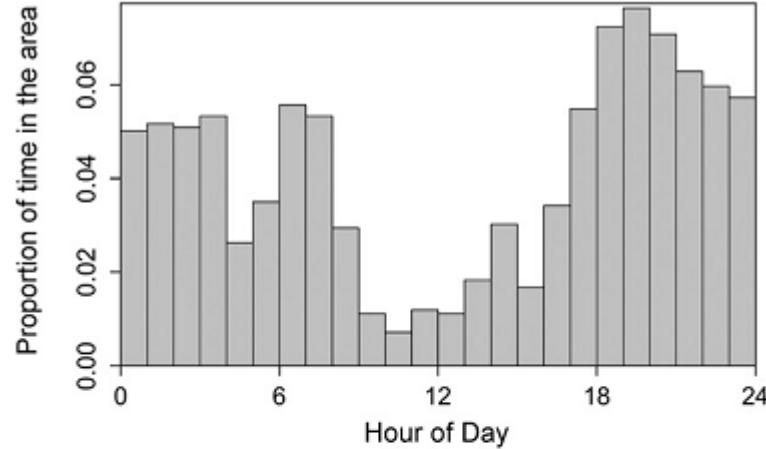


Fig. 4. Wavelet power spectra for the arrival (top) and the presence/absence (bottom) time series. The areas of statistical significance at the 1% and 5% levels are delineated by solid black and gray lines, respectively. The "cone of influence" (striped area) indicates where spectrum values are unreliable due to edge effects. Horizontal dashed black lines represent periods which were significant at the 1% level in the Fourier spectra: 12 h for the arrival time series, and 24 h, 7 days (169 h), and 30 days (720 h) for the presence/absence time series.



Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator

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Ignoring autocorrelation may lead to underestimated ranges

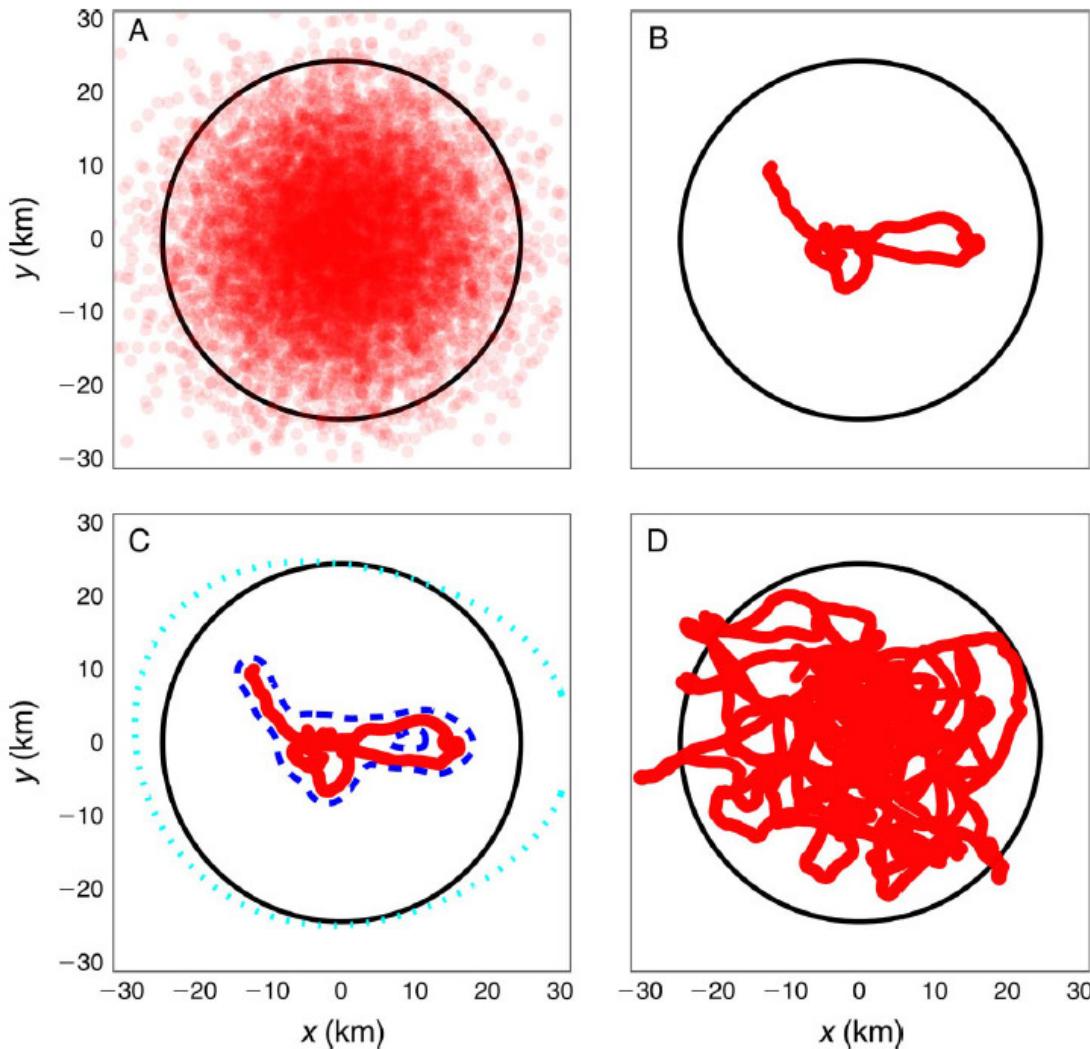


FIG. 1. (A) A simulation of location data points (red dots) drawn from a spatial point process that unrealistically lacks autocorrelation between points. (B) More realistic data drawn from a continuous, stochastic process fit to tracking data for Mongolian gazelle, *Procapra gutturosa* (Fleming et al. 2014a). The true home ranges (95% confidence regions) for the stochastic processes underlying the plots in (A) and (B) are identical (black circles) and in both cases there is an identical number of data points, but in (B) the observation period is only long enough to observe a few home range crossings. (C) The home range area of (B) is estimated using conventional kernel density estimation (KDE; dashed blue line) and our new autocorrelated KDE (AKDE; dotted aqua line). The conventional KDE approach draws tight boundaries around the observed data, while AKDE can project future space use from limited data. (D) The stochastic process from (B) is run 10 times further into the future, demonstrating that AKDE was correct and KDE was incorrect in (C), even though KDE might have seemed reasonable based on visual inspection.

Mongolian gazelles are nomadic wanderers whose movements may involve gross displacements exceeding 1000 km/yr with little concordance among years (Olson et al. 2010, Mueller et al. 2011, Fleming et al. 2014*b*). Consequently, longer observation periods tend to show the gazelles using larger amounts of space, up to an asymptote set by the ACF's details (Fleming et al. 2014*a*). The AKDE captures this important behavior, whereas conventional space-use estimates will miss it because they discard the information encoded in the ACF on the movement process' long-run behavior.

Visually, AKDE estimates often look too large because they contain substantial areas where the focal individual was not directly observed (e.g., Figs. 1 and 2; Appendix B: Eq. B.3). However, as previously men-

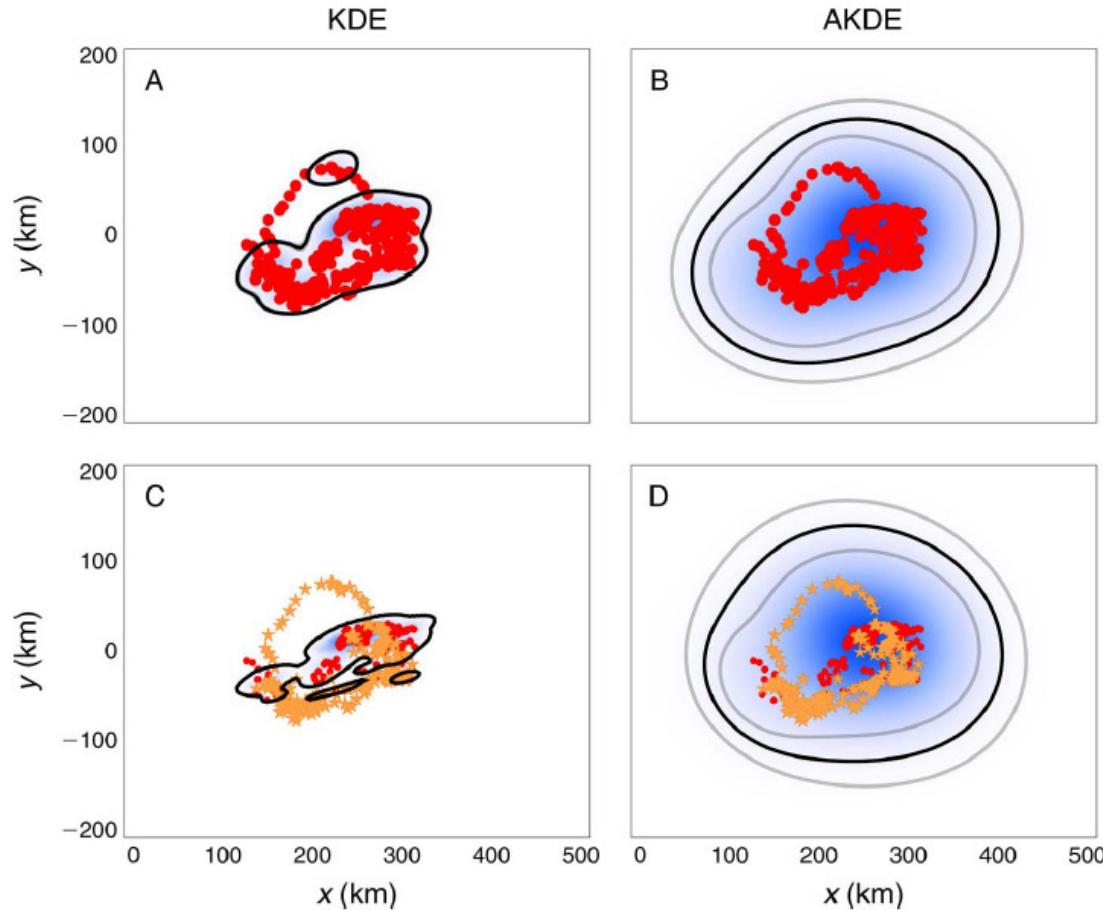


FIG. 2. (A) KDE and (B) AKDE are compared against the distribution of locations (red dots) for a Mongolian gazelle, observed over a period of 361 d. In all cases, the density estimate is shown as blue shading, a black contour line delineates the point estimate of the 95% home range area, and two gray contour lines express the 95% confidence range of the home range area. For AKDE, there is significant uncertainty in delineating how much area the gazelle will use 95% of the time, which is estimated to fall between the two gray contours, while for conventional KDE, the estimated uncertainty is hardly visible. The wide confidence intervals of the AKDE are appropriate for this data set, as will be demonstrated in the final two panels, while KDE massively underestimates the real uncertainty associated with home range estimation. In panels (C) for KDE and (D) for AKDE, the data set is segmented into its first half (red dots) and second half (orange stars), and only the first half is used for both autocorrelation parameter estimation and kernel density estimation. This subsetting has a large effect on the home range predictions from the KDE method, but only a very minor change for the AKDE predictions, given that there is already enough information in the first half of the data to fully represent the movement behavior (but not necessarily the space use). The KDE method fails to anticipate the possibility of the long sojourns that the gazelle undertook during the second half of the monitoring period. This possibility was already accounted for by the AKDE method, which was well informed by the autocorrelation structure present in the first half of the data. Traditional leave-one-out cross-validation assumes independence and does not cross-validate the data in such a temporally meaningful way.

All clear ... as mud?
Let's do the practical!

