

AniMove 2023
Kelowna, BC, Canada

Habitat Selection Analysis

Tal Avgar



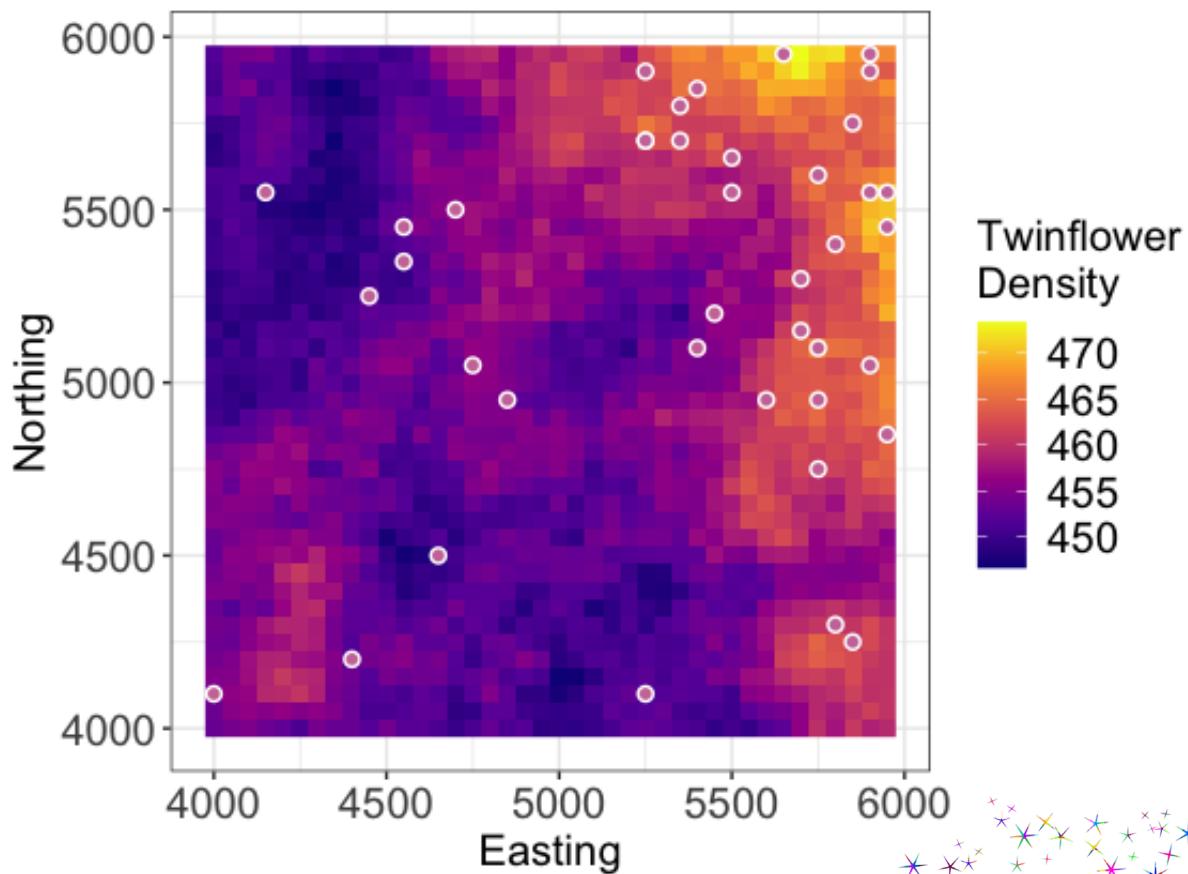
What is ‘habitat’?

- ❖ Geographic space (G-Space)
 - ❖ 1-3 isotropic dimensions
 - ❖ Orthogonal or spherical projection

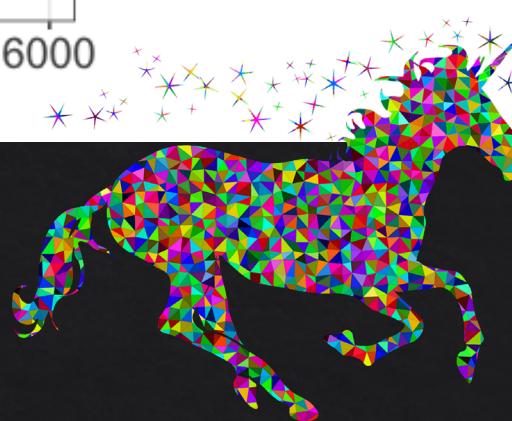
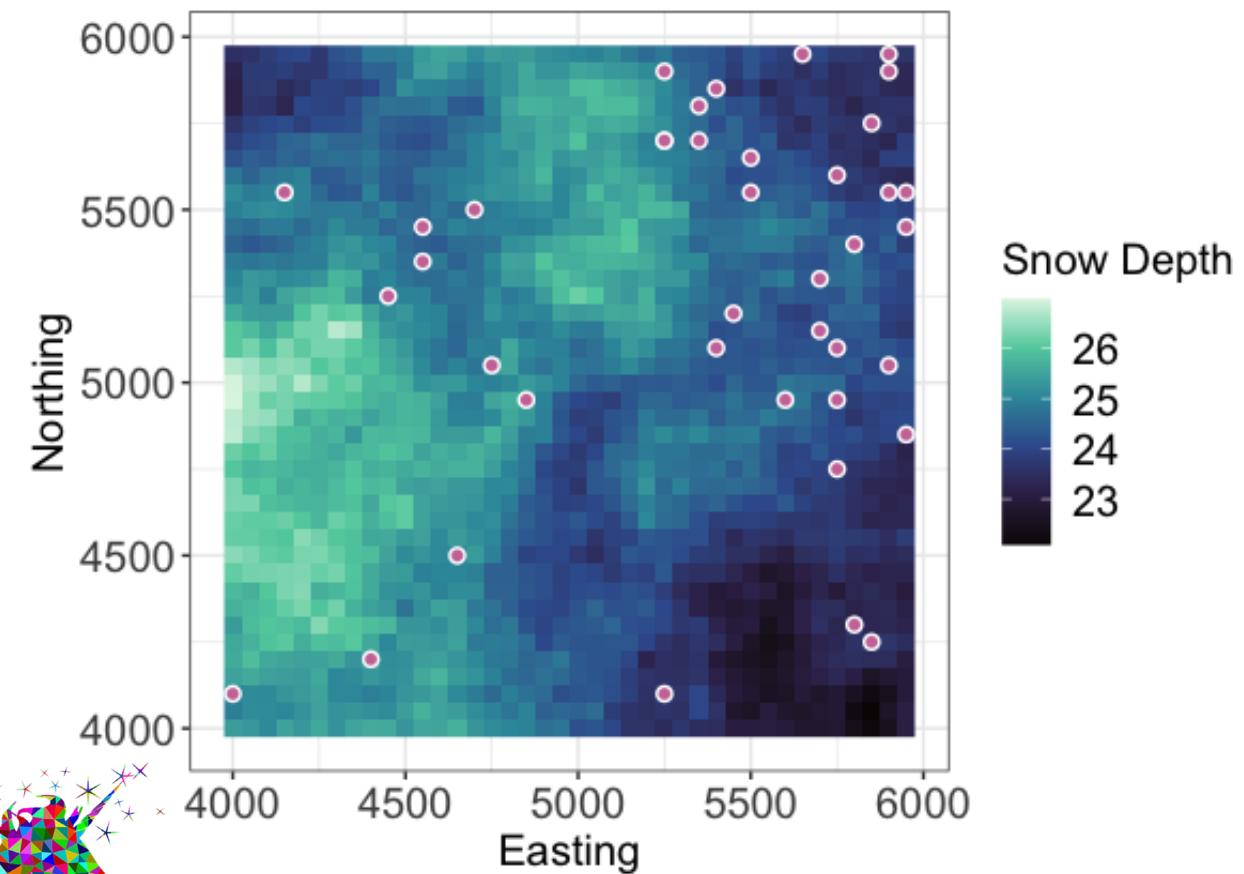
What is ‘habitat’?

- ❖ Geographic space (G-Space)
 - ❖ 1-3 isotropic dimensions
 - ❖ Orthogonal or spherical projection
- ❖ Environmental space (E-Space)
 - ❖ Any number of dimensions, each an attribute of the environment (habitat variable)
 - ❖ Habitat variables are either continuous or binary (including ‘categorical variables’ - a set of mutually exclusive binary variables – one for each category)
 - ❖ 3 types of habitat variables: Resources (more is better; depletable), Risks (less is better; dilutable), and conditions (intermediate may be best; non-depletable)

Resource in Geographic Space



Condition in Geographic Space



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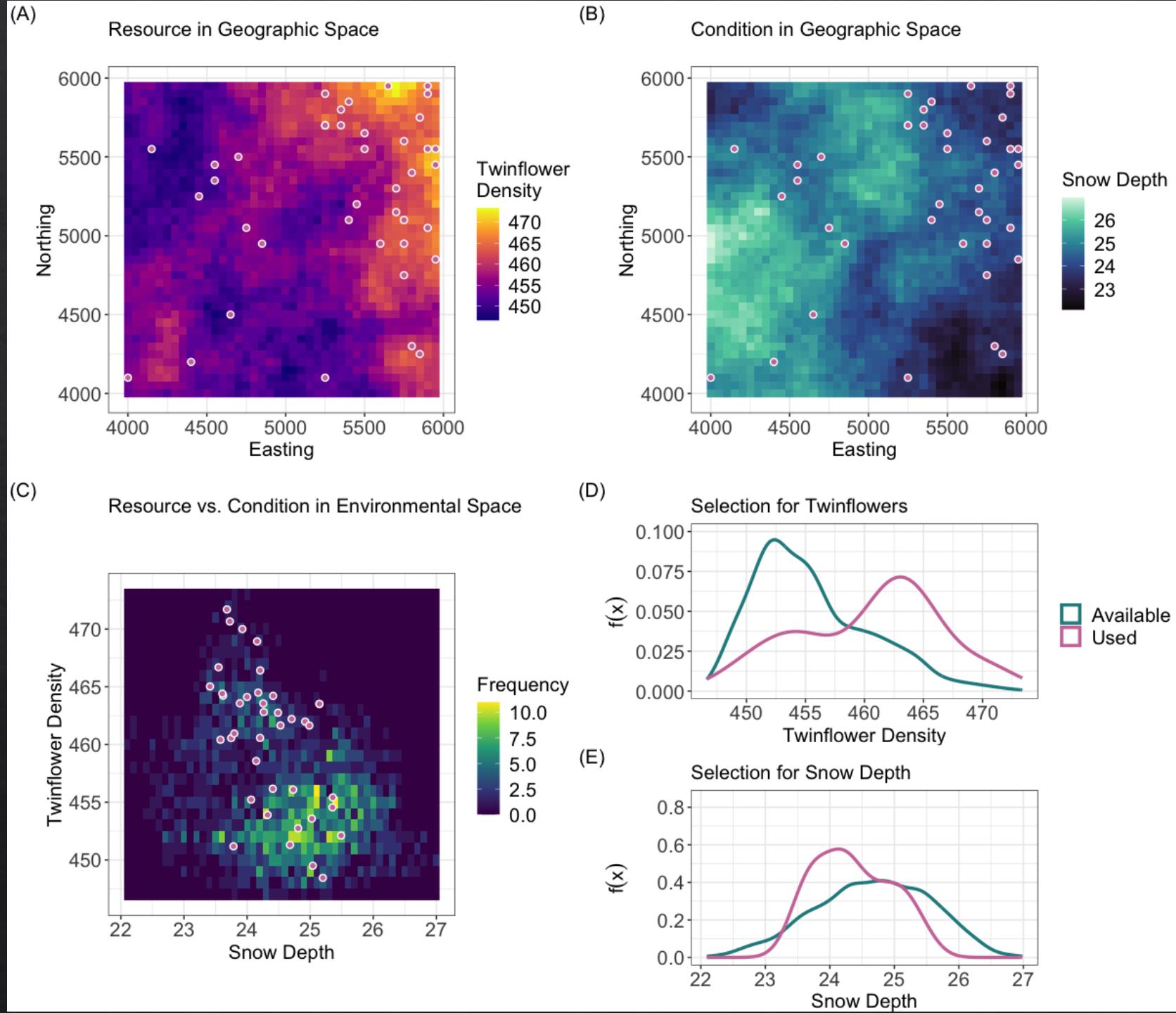
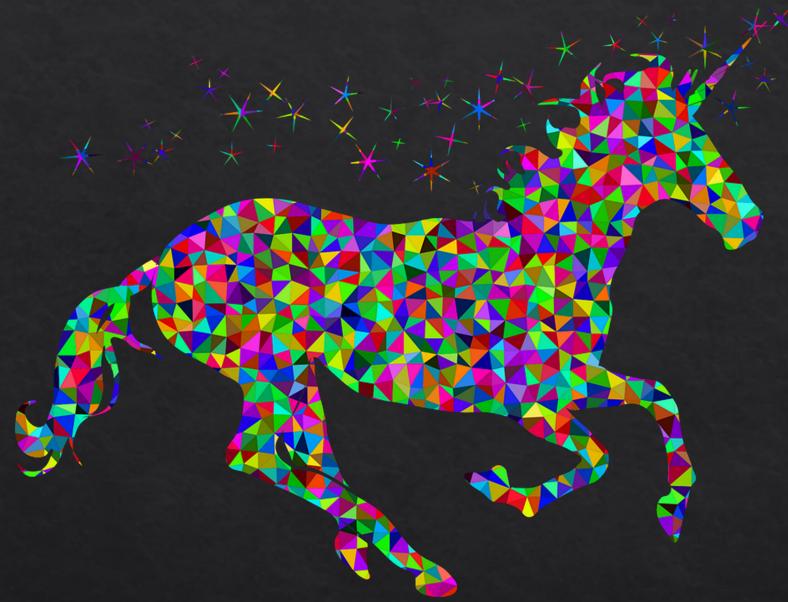
- ❖ Habitat: a unique point or sector in E-Space
- ❖ Habitat Unit: a discrete, environmentally homogeneous, sector of G-Space

What is ‘habitat’?

- ❖ Habitat: a unique point or sector in E-Space
- ❖ Habitat Unit: a discrete, environmentally homogeneous, sector of G-Space
 - ❖ A unique point in G-Space (a habitat unit) could be mapped to a unique point in E-Space, but the opposite is not necessarily true; a unique point in E-Space could be mapped to any number of habitat units in G-Space (including none)

What is ‘habitat selection’?

The use of a given habitat (in E-Space) more often than would be expected based on the availability of its units (in G-Space)



Presence, Absence, Use, and Availability

- ❖ A habitat unit was ‘used’ if the animal was present there; presence (or ‘occurrence’ or ‘occupancy’) is commonly observable

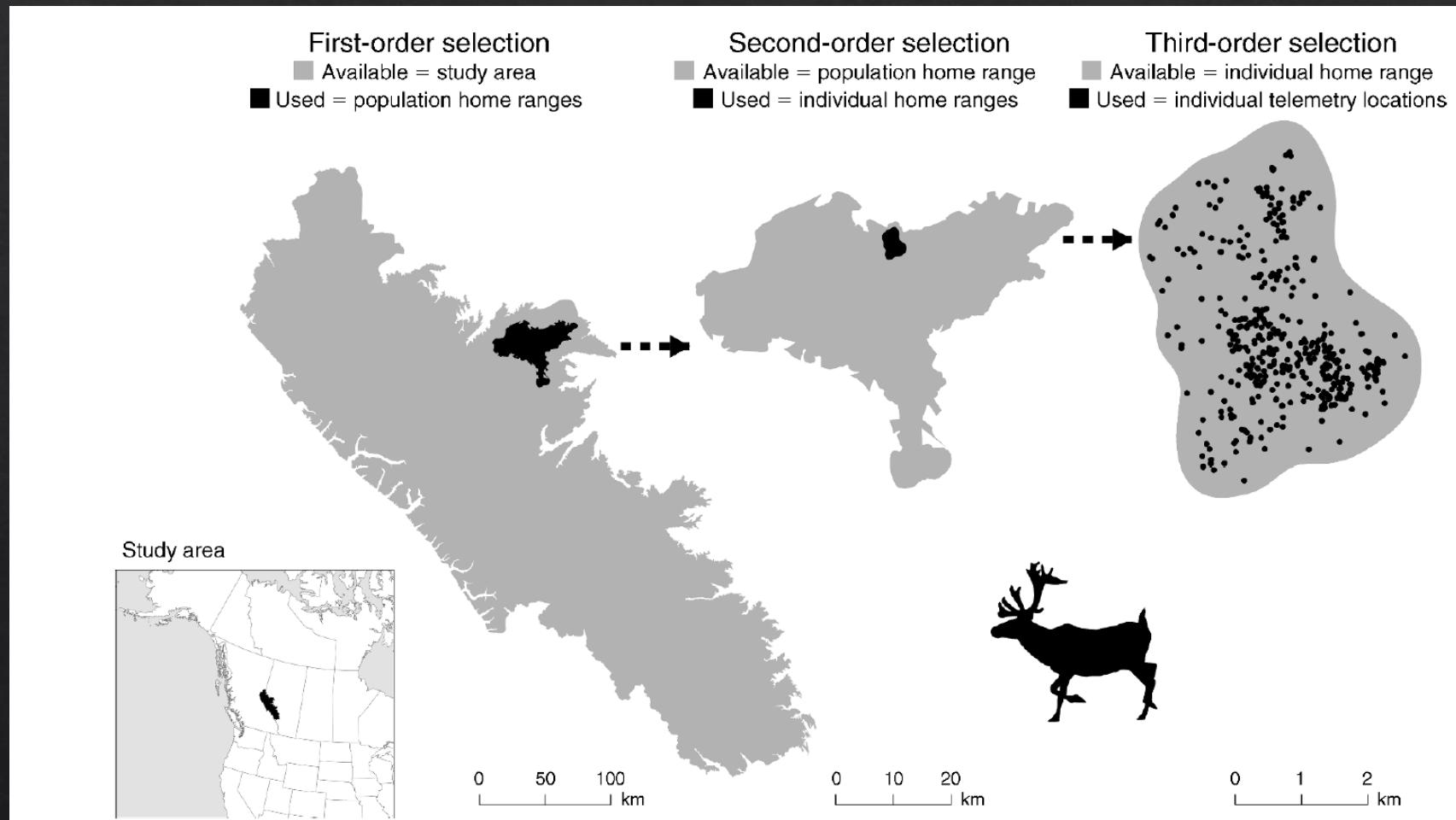
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- ❖ In the absence of absence, usage is contrasted with availability ('background'/'pseudoabsence'/'contaminated absence'/'control')
 - ❖ A point was ‘available’ if the animal could have used it
 - ❖ The ‘availability domain’ is an area (in G-Space) across which the animal is equally likely to be in the absence of habitat selection

What is available?



Johnson, D.H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, 65–71.

Decesare, N.J., et al. (2012). Transcending scale dependence in identifying habitat with resource selection functions. *Ecology*, 22, 1068–1083.

What is available?

But what if availability varies across space or time?



Poisson Spatial Point Pattern

- ❖ A spatial Poisson point pattern is a collection of points randomly scattered through space such that their positions are independent and identically distributed (*iid*)

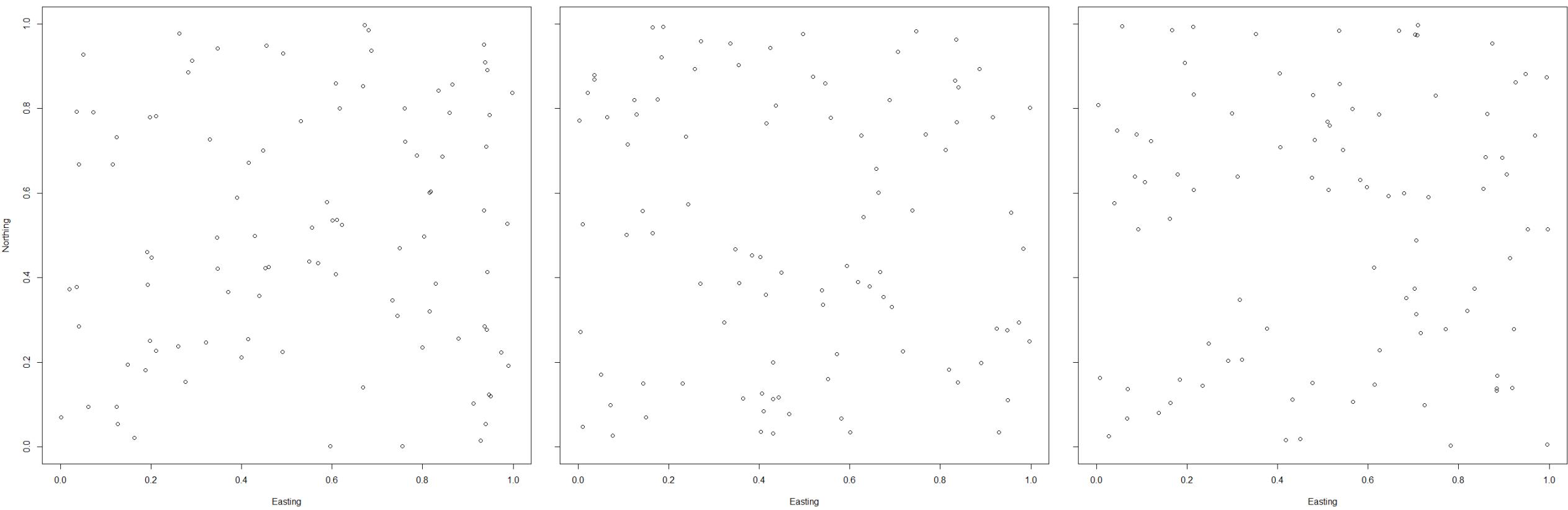
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- ❖ A Poisson SPP could be *homogeneous* (the intensity is constant – it does not vary through space)

```
> A <- 1  
> n <- rpois(1, lambda=100)  
> plot(runif(n*A)*sqrt(A), runif(n*A)*sqrt(A),  
      xlim=c(0, sqrt(A)), ylim=c(0, sqrt(A)),  
      xlab='Easting', ylab='Northing')
```



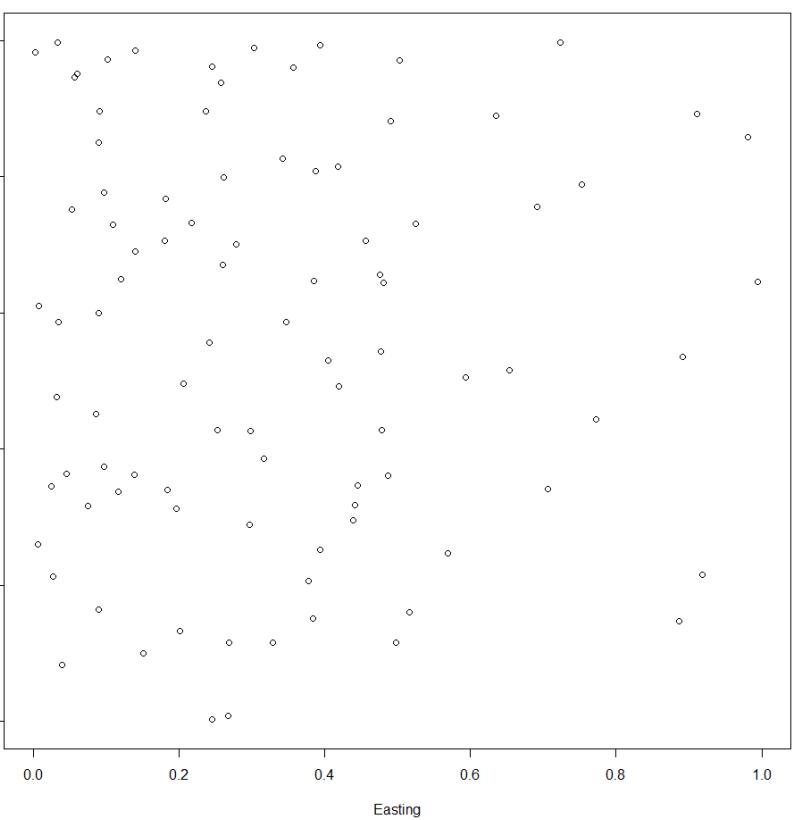
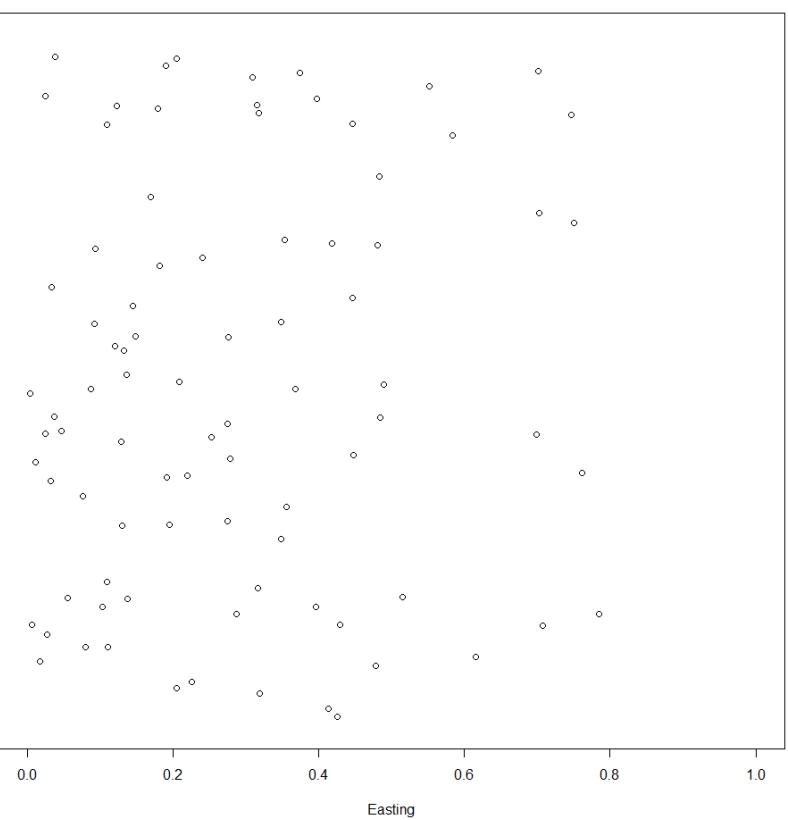
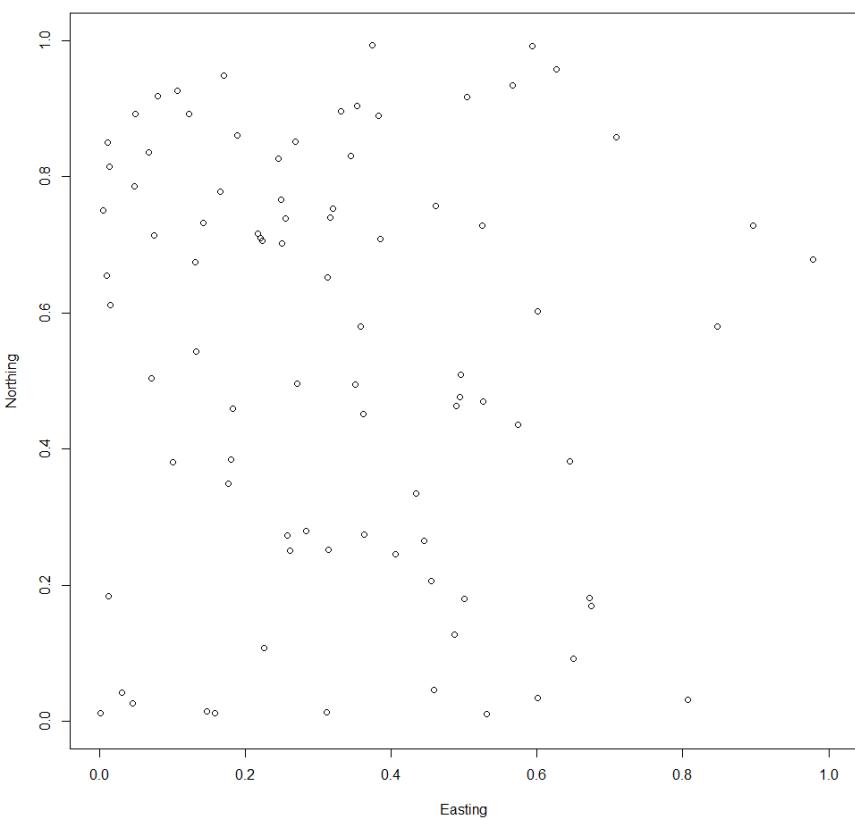
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- ❖ A Poisson SPP could be *homogeneous* (the intensity is constant – it does not vary through space) or *inhomogeneous* (the intensity varies through space)

```

> A <- 1
> n <- rpois(1, lambda=100)
> plot(rbeta(n*A, 1, 2)*sqrt(A), runif(n*A)*sqrt(A),
      xlim=c(0, sqrt(A)), ylim=c(0, sqrt(A)),
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```



Inhomogeneous Poisson SPP

The Poisson intensity, λ , at location x is given by:

$$\lambda(x) = E(N) \cdot \frac{\exp\left(\sum_{j=1}^m [\beta_j \cdot h_j(x)]\right)}{\int_A \exp\left(\sum_{j=1}^m [\beta_j \cdot h_j(x)]\right) dx} = \exp\left(\ln[E(N)] + \sum_{j=1}^m [\beta_j \cdot h_j(x)] - c\right)$$

where $E(N)$ is the expected number of individual across a spatial (availability) domain of size A , and β_j is the parameter linking the relative intensity in x to the local value of the j 's (out of m) habitat variables, $h_j(x)$



One ring to rule them all,
One ring to find them,
One ring to bring them all
and in the darkness bind them.

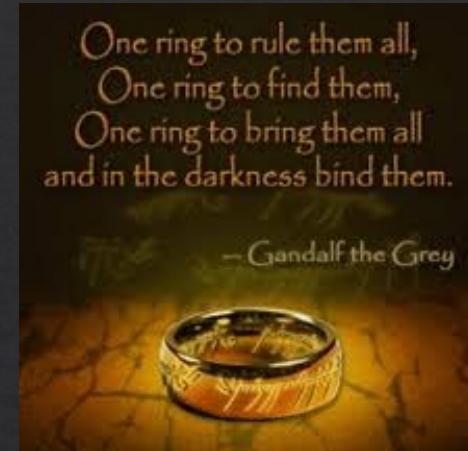
—Gandalf the Grey

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$$\text{where } c = \ln \left[\int_A \exp(\sum_{j=1}^m [\beta_j \cdot h_j(x)]) dx \right]$$



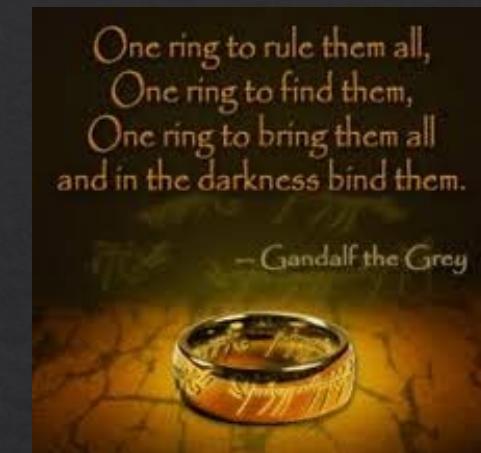
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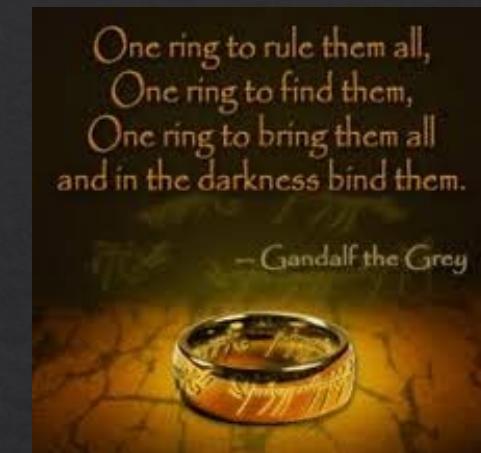


The probability that location x is ‘used’ is the same as the probability that the number of individuals, n , within an area a centered at x is > 0 :

$$\text{prob}[n(x) > 0 | \lambda(x), a] = 1 - \exp[-\lambda(x) \cdot a]$$

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If $|\lambda(x) \cdot a| \ll 1$:

$$1 - \exp[-\lambda(x) \cdot a] \approx \lambda(x) \cdot a$$



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eHSF

An inhomogeneous Poisson SPP:

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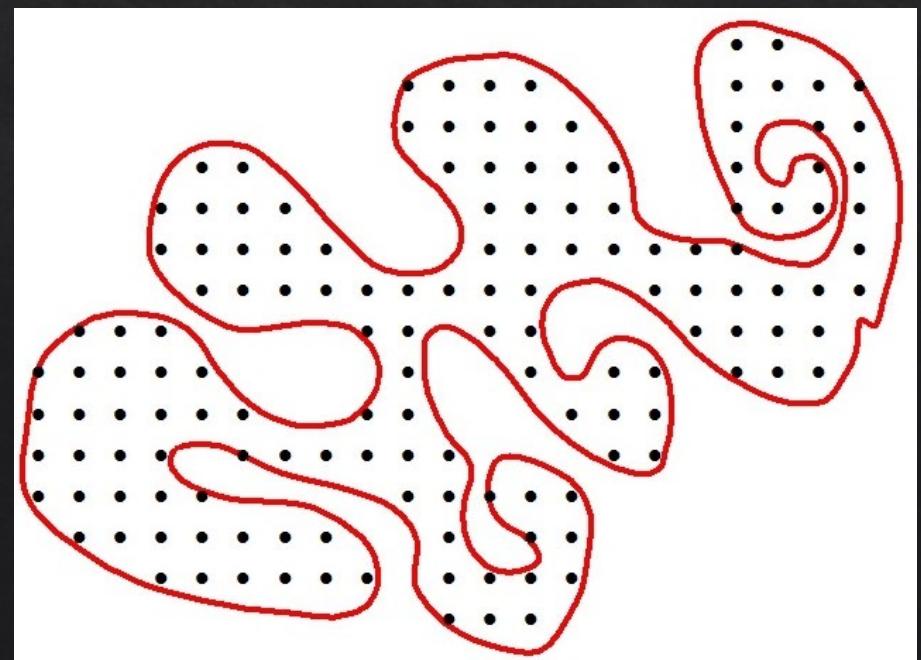
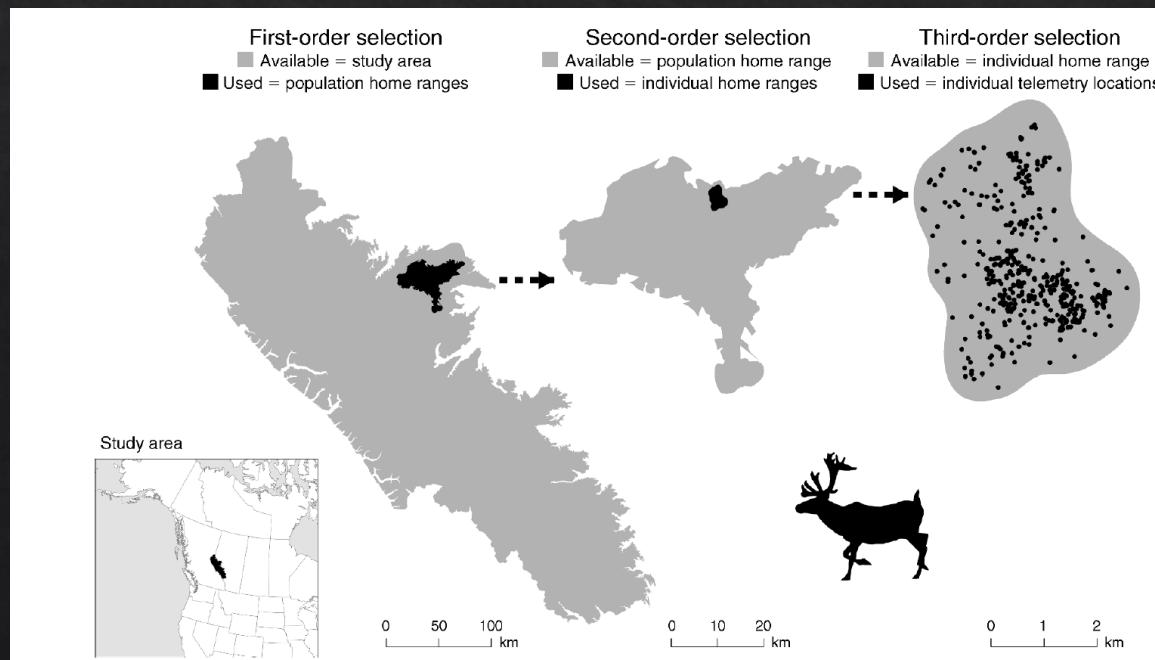
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Given a set of ‘presence-only’ data and an availability domain, maximum-likelihood estimates of the ‘selection coefficients’ $\{\beta_1, \dots, \beta_j, \dots, \beta_m\}$ are obtained via logistic regression (a Binomial GLM) with a response variable of either 1 (‘used’) or 0 (‘available’)

Sampling available points ($|\lambda(x) \cdot a| \ll 1$)

Once an availability domain is delineated:

- ❖ Sample as many available points as computationally feasible
- ❖ Assign a large weight to each available point and a weight of 1 to all used points
- ❖ Sample available points uniformly across the domain



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The absolute intensity of the process remains unknown ($\ln[E(N)]$) is unidentifiable because we cannot separate it from c and $\ln[a]$); β_0 (the so called ‘intercept’) is a nuisance parameter; the resulting exponential Habitat Selection Function (eHSF) is only proportional to the probability of use

$$w(x) = \exp\left(\sum_{j=1}^m [\beta_j \cdot h_j(x)]\right) \propto \text{prob}[n(x) > 0]$$

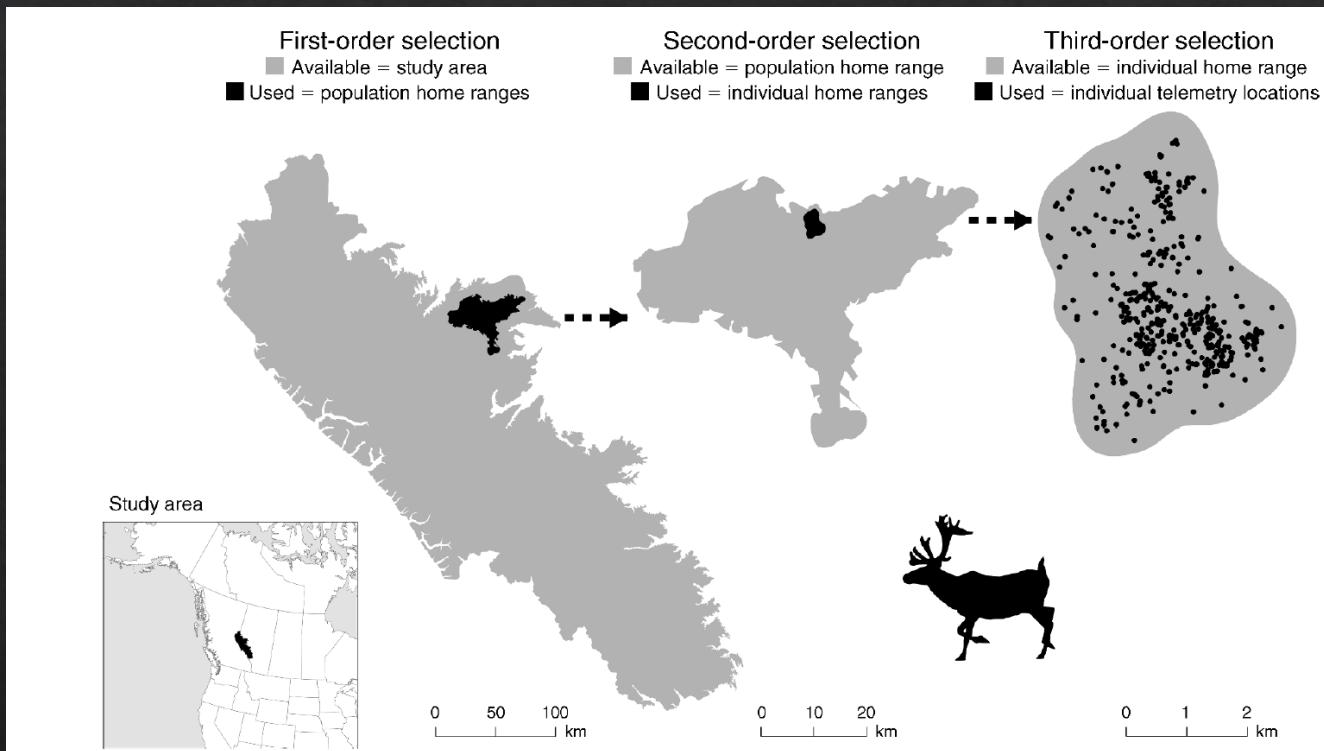


‘scale’

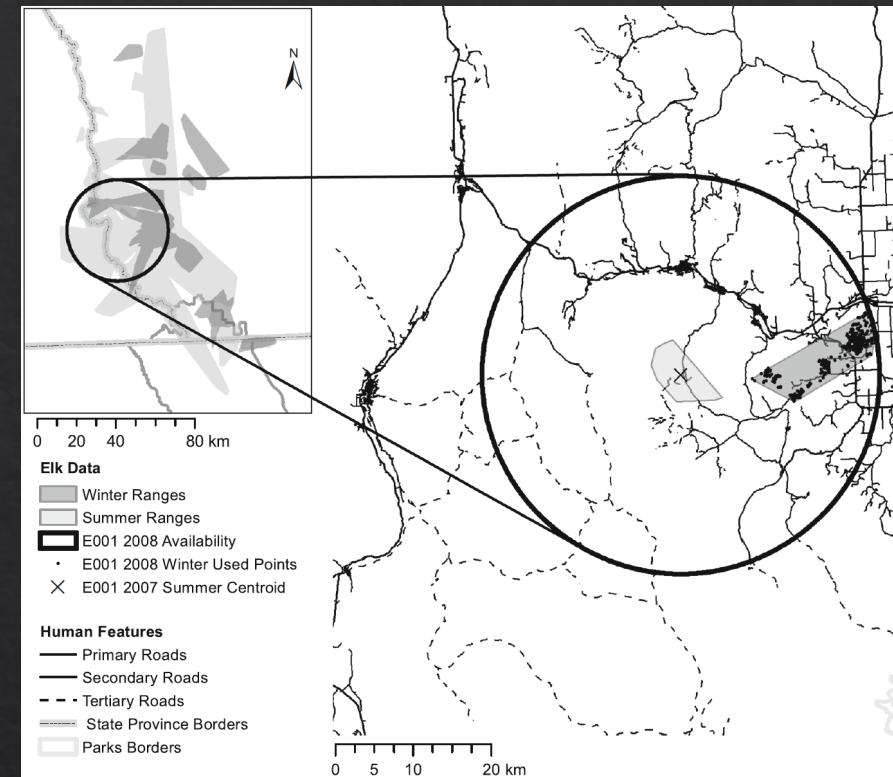
- ❖ **Spatial Extent:** the overall area encompassed by the analysis
- ❖ **Spatial Grain:** the size of a single habitat unit
- ❖ **Temporal Extent:** the duration/seasons encompassed by the analysis
- ❖ **Temporal Grain:** the time gap between observations (frequency of relocations)



Spatial Extent



What's the Question?



Covariate	Within-home-range			Among-home-range		
	Mean	Lower CI	Upper CI	Mean	Lower CI	Upper CI
Elevation	0.0018	0.0009	0.0028	-0.0078	-0.0088	-0.0069
Normalized NDVI	0.2698	0.1723	0.3804	0.8514	0.6807	1.0386
Normalized NDVI ²	-0.0062	-0.0083	-0.0043	-0.0178	-0.0218	-0.0141
InPrimaryRoadDist	0.1283	0.0021	0.2680	0.2749	0.1680	0.3941
InSecondaryRoadDist	0.4590	0.3788	0.5368	0.4417	0.3393	0.5489
InTertiaryRoadDist	0.1386	-0.0336	0.3098	0.7605	0.6039	0.5489

Spatial Grain

Why manipulate the spatial grain?

- ❖ unify the spatial grain among various variables
- ❖ reflect uncertainty in the variables
- ❖ reflect uncertainty in the position of the animal
- ❖ reflect selection for mixed habitat or habitat edge
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Stationarity ('steady state'): space-use behavior and its environmental drivers are assumed to remain unchanged through the temporal (and spatial) extent of the study

- ❖ Seasonality
- ❖ Disturbance
- ❖ Resource depletion
- ❖ Population dynamics
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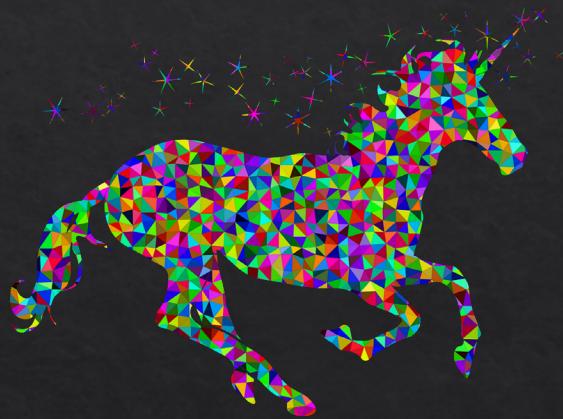
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- ❖ Use iSSF (we'll get there)
- ❖ Use autocorrelation-informed weighting [Alston, J. M., Fleming, C. H., Kays, R., Streicher, J. P., Downs, C. T., Ramesh, T., Reineking, B., & Calabrese, J. M. (2023). Mitigating pseudoreplication and bias in resource selection functions with autocorrelation-informed weighting. *Methods in Ecology and Evolution*, 14, 643–654]

it's R time!



https://github.com/jmsigner/movement_workshop_spring_2023

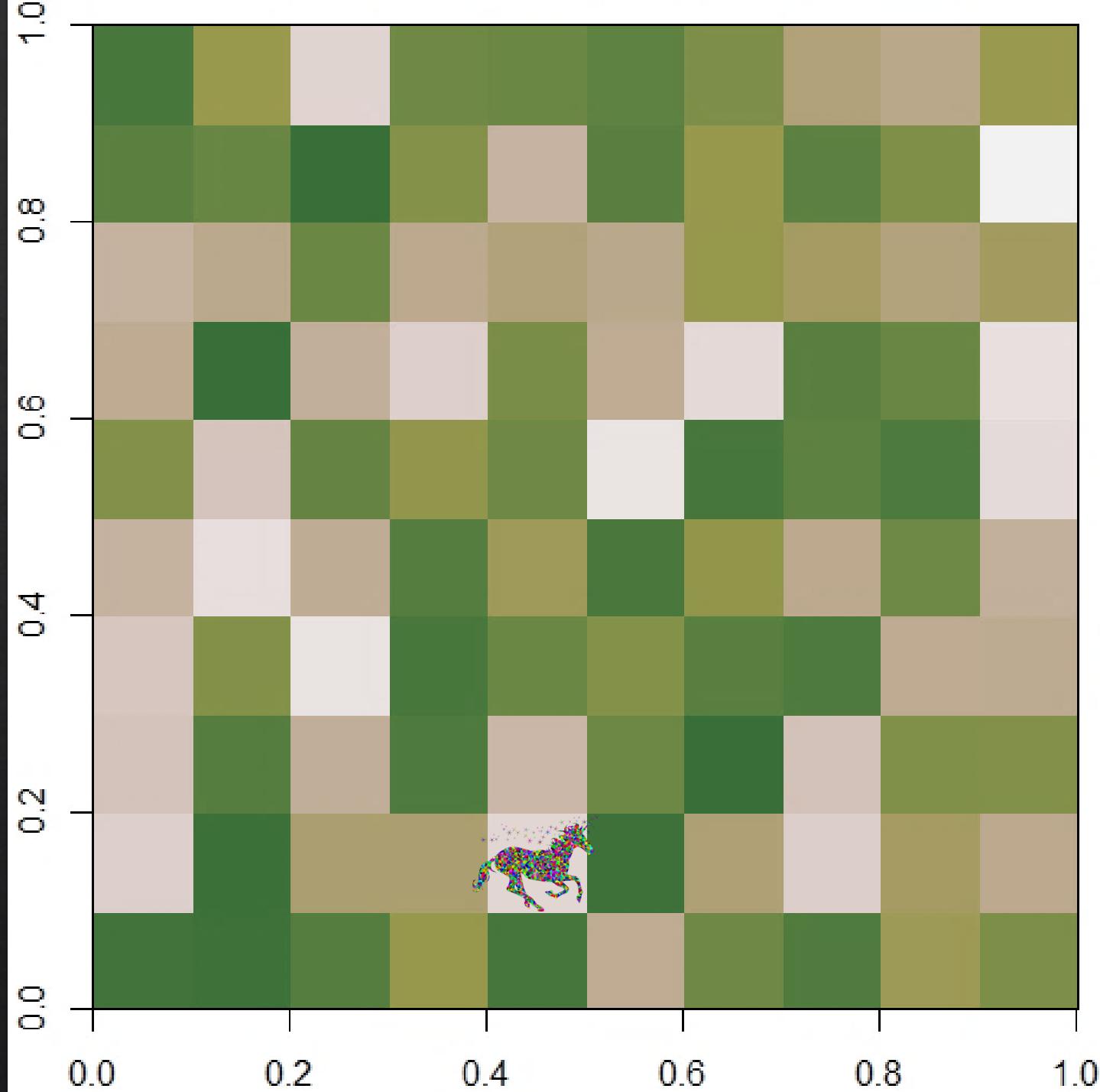
integrated Step-Selection Function (iSSF)

Simultaneously modelling movement and habitat selection by
parametrizing a *Locally Biased Correlated-Random Walk*

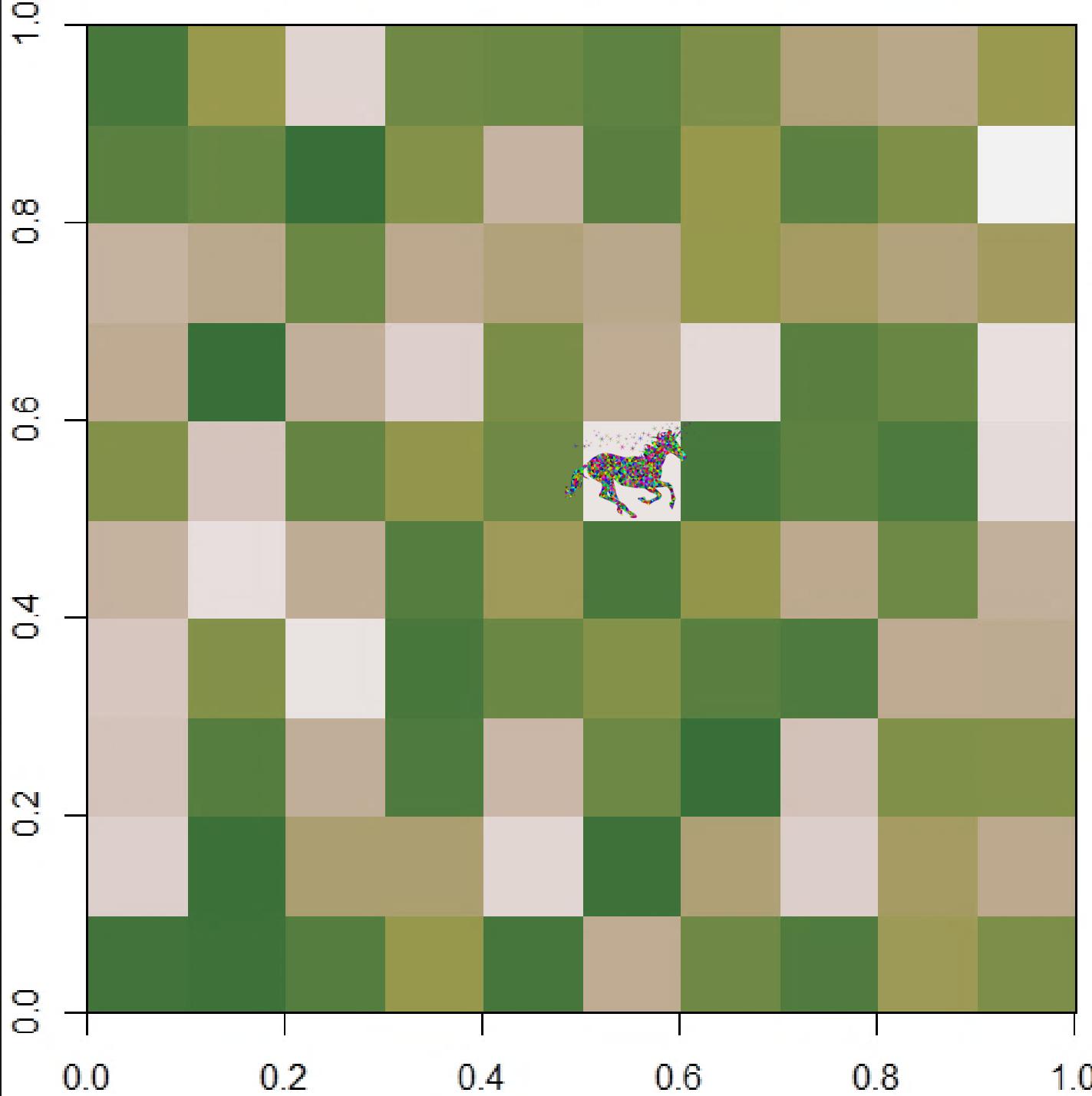
Locally Biased Correlated-Random Walk

- ❖ A discrete-time positional-jump process

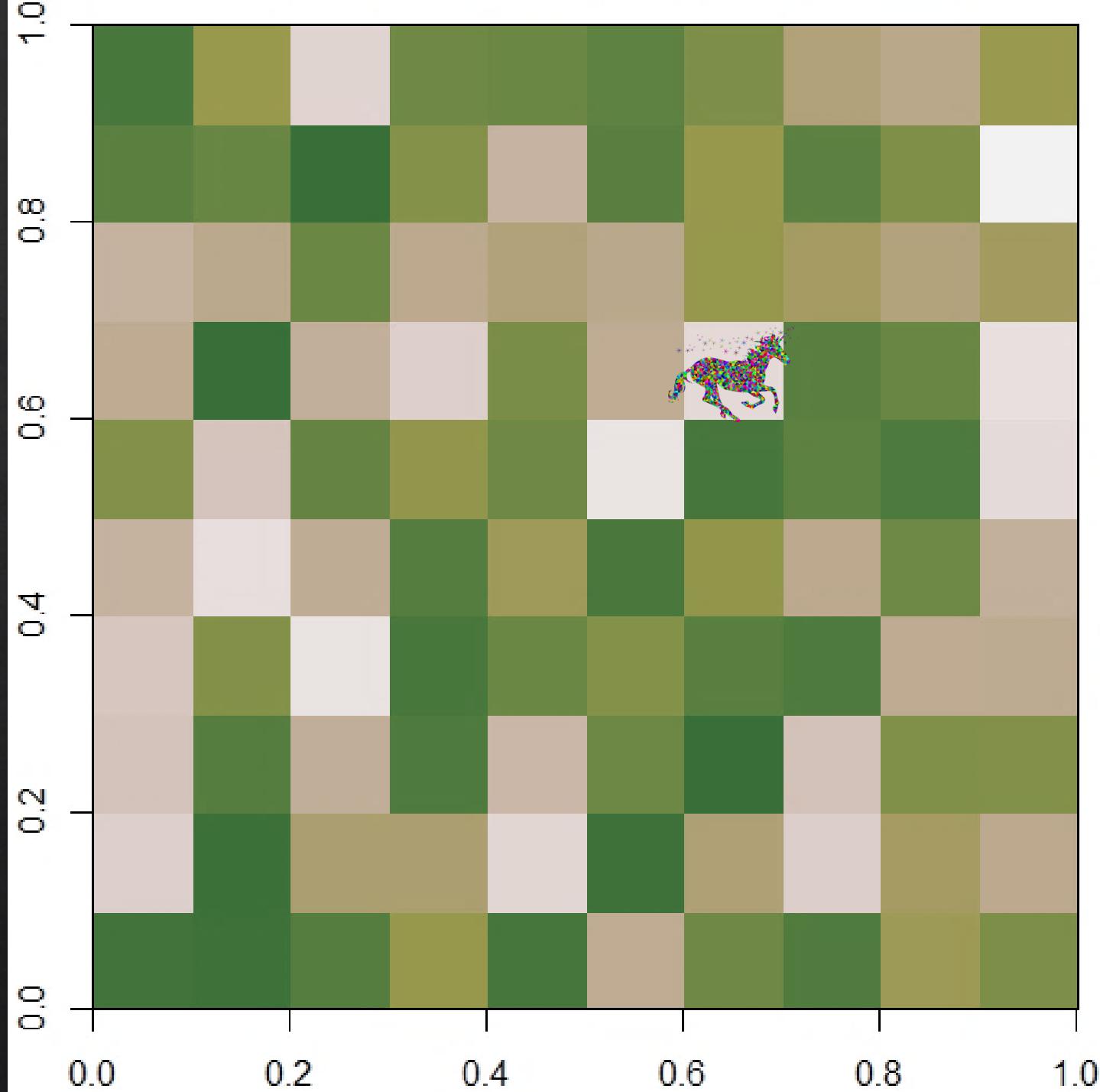
$t = 1$



$t = 2$



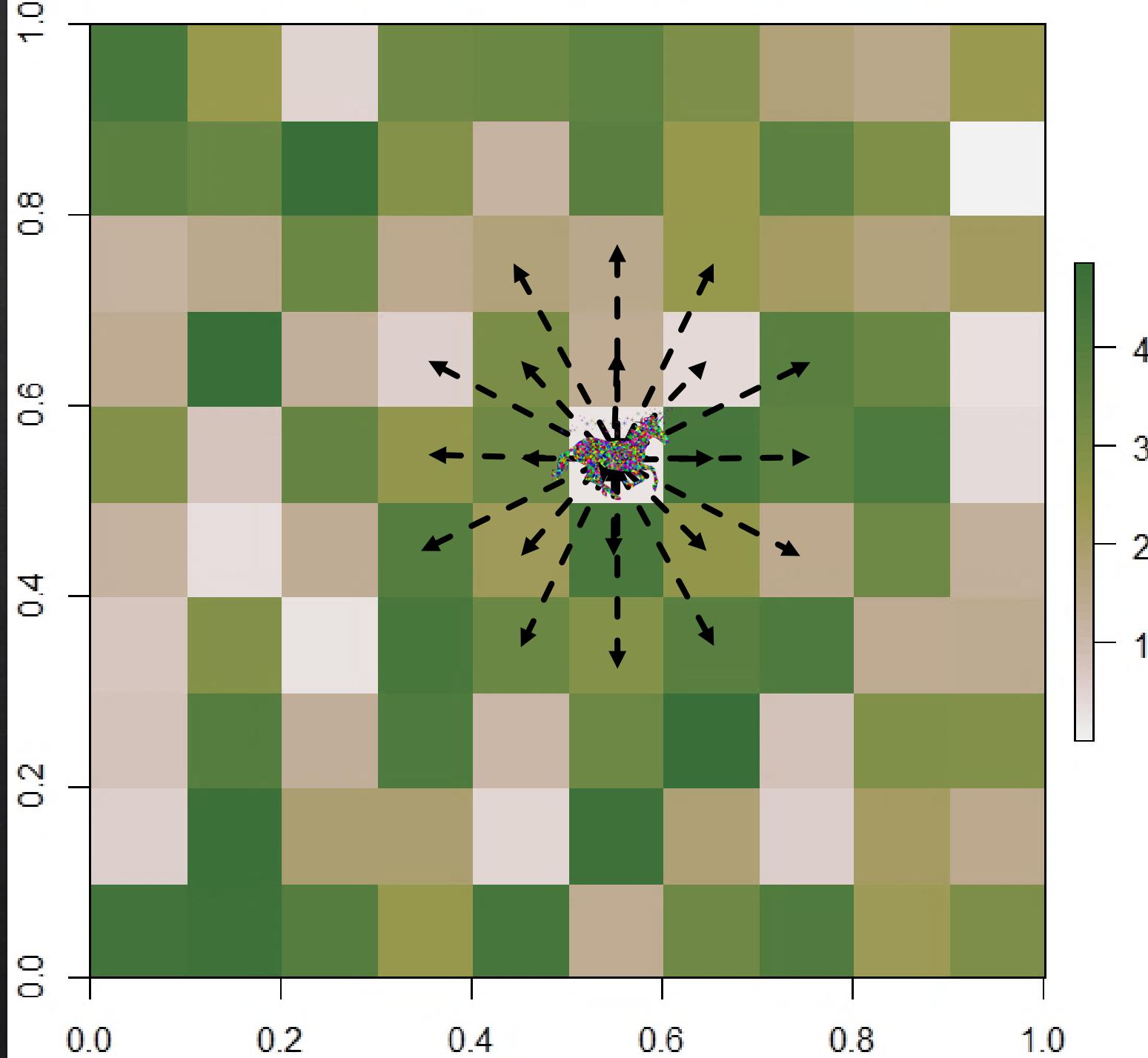
$t = 3$



Locally Biased Correlated-Random Walk

- ❖ A discrete-time positional-jump process
- ❖ Jump (step) length is a random variable drawn from a parametric step-length distribution, with parameters that may depend on space (due to environmental conditions at the step's start-point; e.g., due to deep snow), time (e.g., due to circadian rhythm), and/or the previous step's length (temporal autocorrelation)

$t = 2$

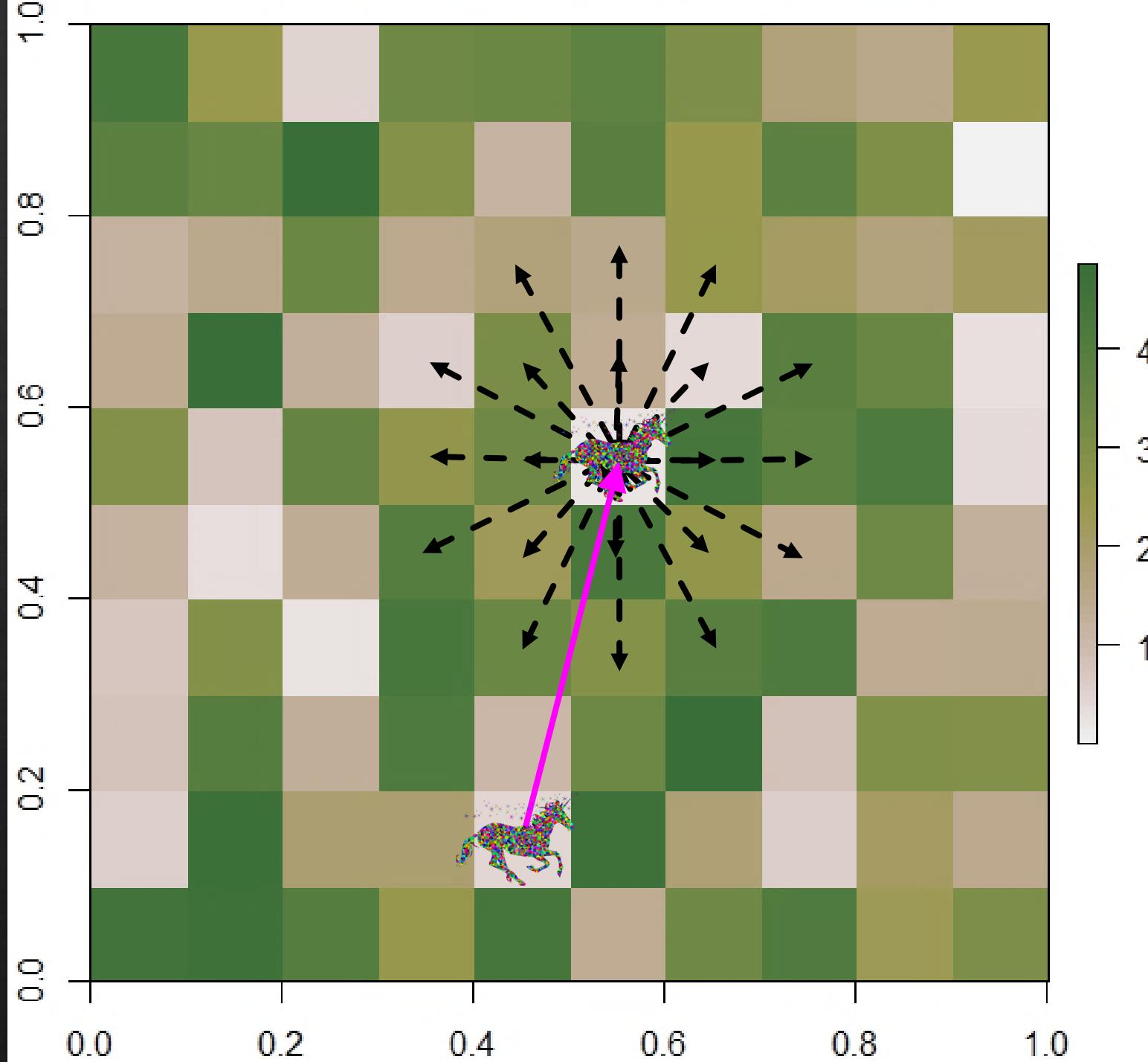


40
30
20
10

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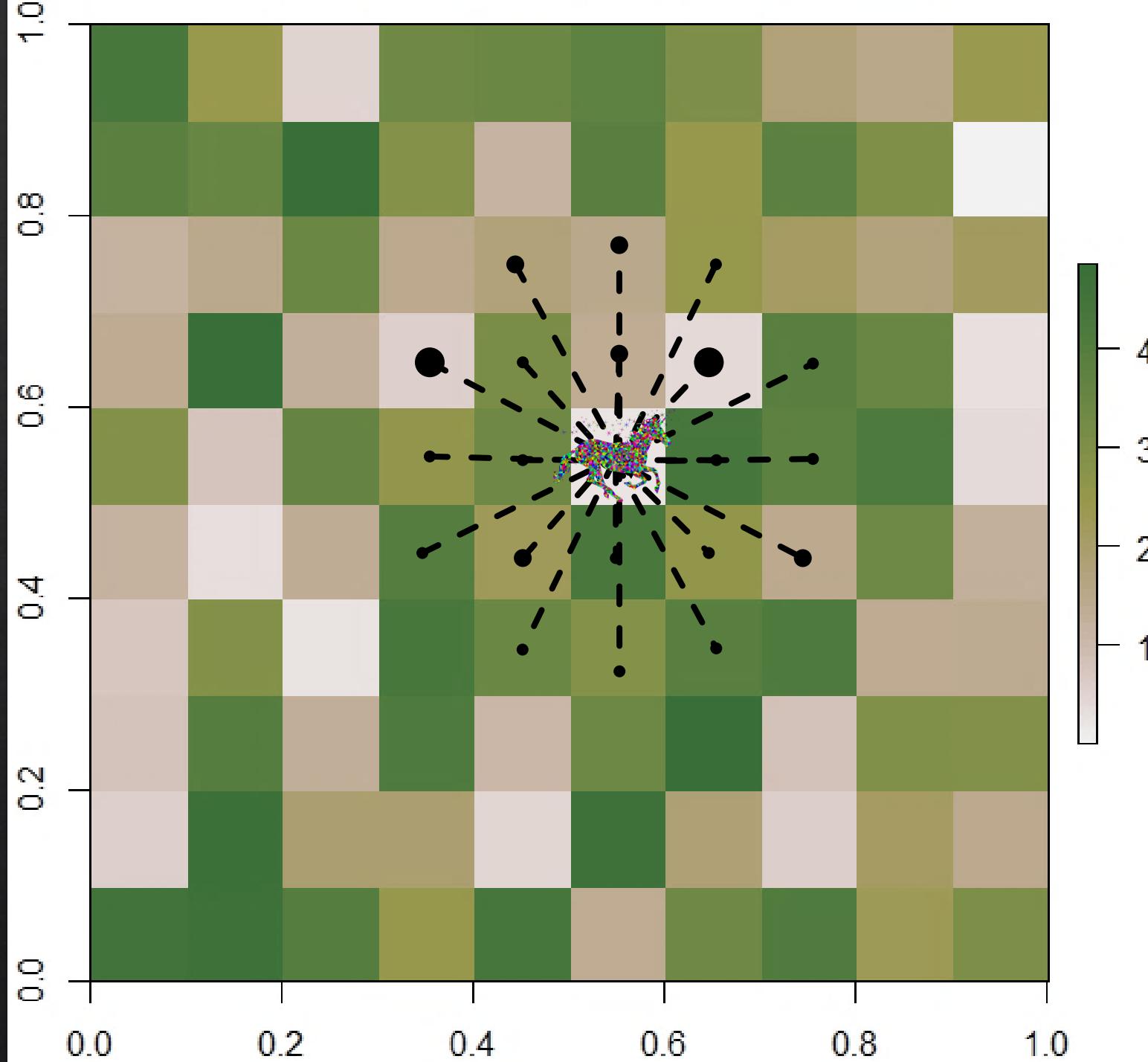


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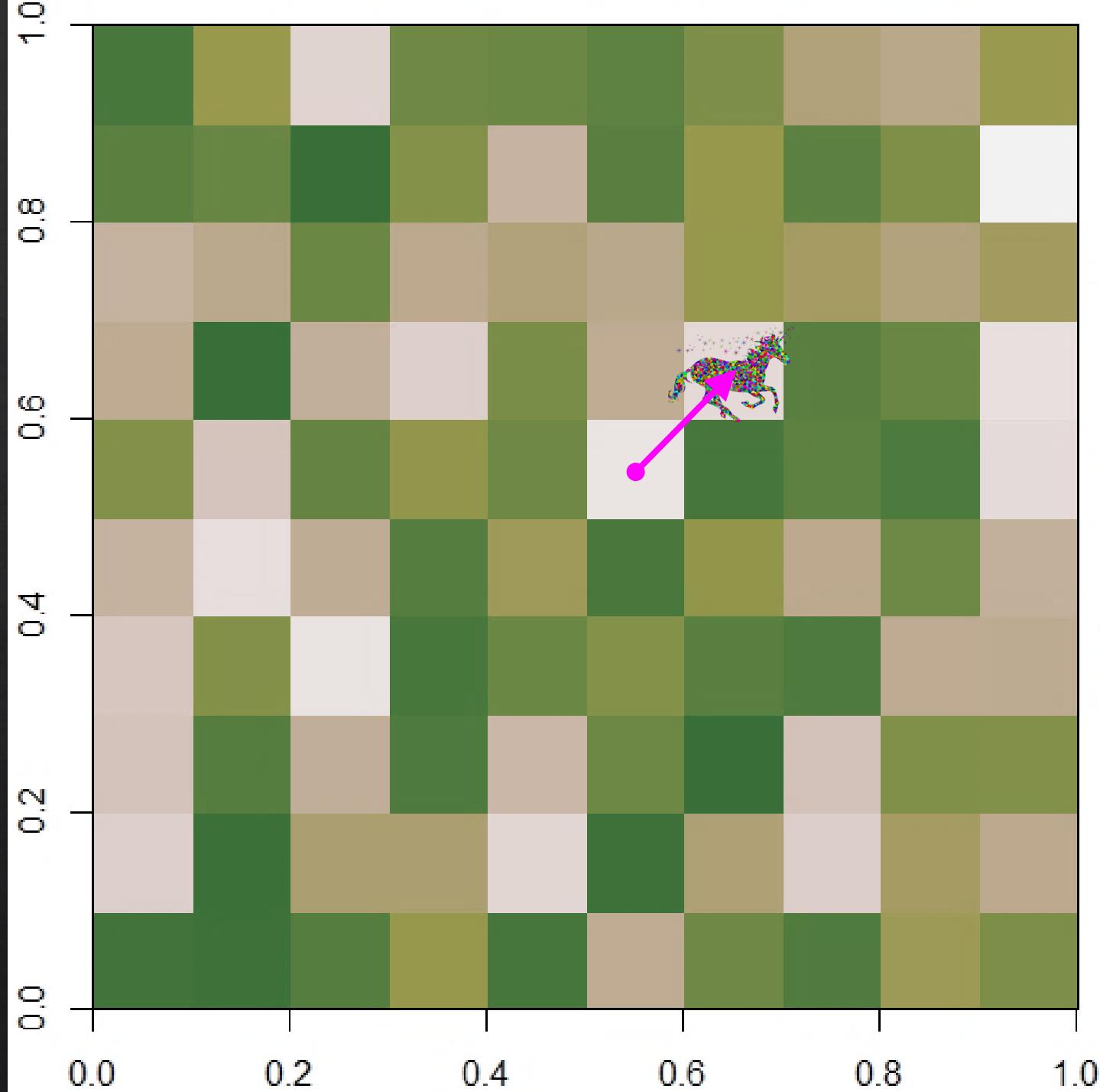
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- ❖ The step's end-point in environmental space (the habitat) is a random variable drawn from a selection-weighted distribution of available habitats. Habitat selection strength may vary in space and/or time

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- ❖ Straightforward hypotheses evaluation, including complex temporal dynamics
- ❖ Resolves many (but not all) statistical issues with temporal autocorrelation



iSSF in practice

1. **Sample**
2. **Attribute**
3. **Analyze**
4. **Infer**

iSSF in practice

1. Sample
2. Attribute
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- Clean your data ()
- Make sure all steps used in the analysis have the same step duration
- Consider removing ‘non-movement’ steps

https://github.com/jmsigner/movement_workshop_spring_2023

iSSF in practice

1. **Sample:** create *clusters* by matching each *used step* with a set of *available steps* randomly sampled from tentative analytical distributions of step-lengths and turn-angles; these clusters (AKA *strata*) form the basic units of replication

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 - Four possible step-length distributions
 - ◊ Exponential (include *step length* as a covariate)
 - ◊ Half-Normal (include $[step\ length]^2$)
 - ◊ Log-Normal (include $\text{LOG}[step\ length]^2$ and possibly $\text{LOG}[step\ length]$)
 - ◊ Gamma (include *step length* and/or $\text{LOG}[step\ length]$)

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 - Four possible step-length distributions
 - Turn-angle distribution: von Mises (include $\text{COS}[turn\ angle]$ as a covariate)

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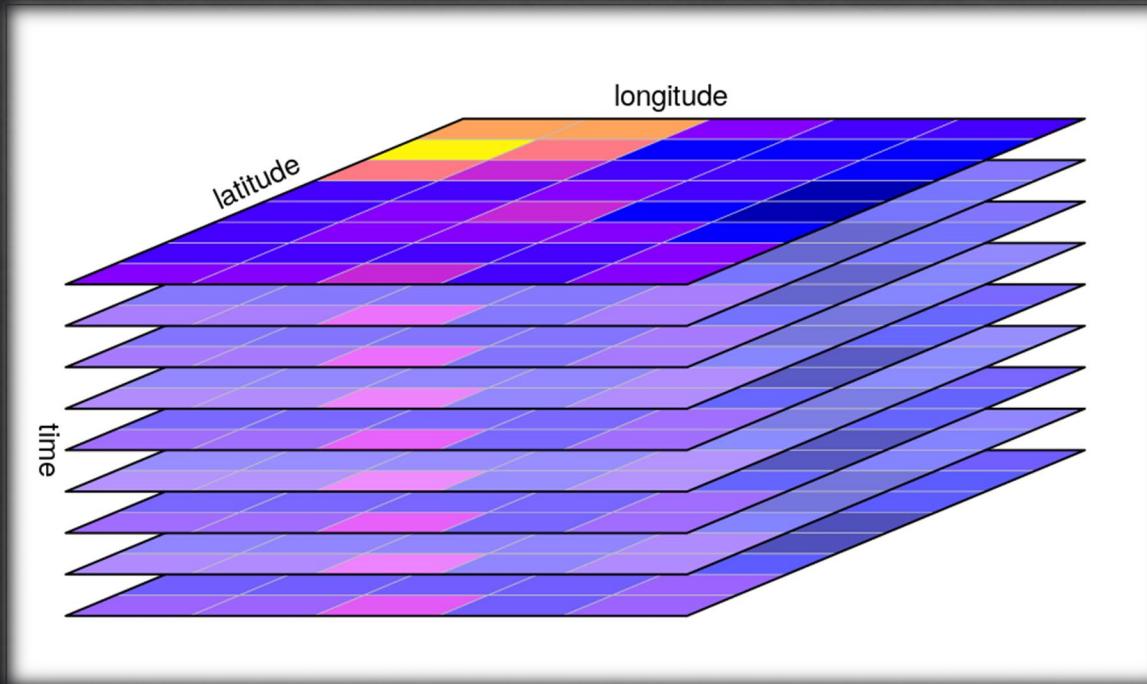
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 - There is no ‘right’ number of available steps; at least one, the more the merrier

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1. Sample
2. **Attribute:** for each step (used and available) extract and append the step's length (and possibly its turn angle), as well as any environmental variable of interest (including temporally dynamic variable)



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 - Attributes that are extracted at the step's start-point (and hence do not vary among steps within a cluster; including temporal variables) can still be used as interactions with movement and/or habitat-selection variables

iSSF in practice

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 - Prediction: selection for water increases when it is hot
Interaction: $\text{temperature_start} \times \text{water_end}$

iSSF in practice

1. **Sample**
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4. **Infer:** use standard inferential tools to evaluate hypotheses regarding habitat selection and/or movement

iSSF in practice

1. **Sample**
2. **Attribute**
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4. **Infer:** use standard inferential tools to evaluate hypotheses regarding habitat selection and/or movement
 - The selection-free movement kernel is obtained by updating the tentative step-length and turn-angle distributions using the corresponding coefficient estimates

If available step lengths were sampled from an exponential distribution with tentative rate parameter λ_0 , and the step length (l) was included as a covariate in the analysis, with resulting coefficient estimate β_l , the adjusted (selection-free) step length Exponential rate parameter is given by:

$$\hat{\lambda} = \lambda_0 - \beta_l$$

If available step lengths were sampled from a half-Normal distribution with scale parameter (standard deviation) σ_0 , and the squared step length (l^2) was included as a covariate in the analysis, with resulting coefficient estimate β_{l^2} , the adjusted (selection-free) step length half-Normal scale parameter is given by:

$$\hat{\sigma} = \frac{\sigma_0}{\sqrt{1 - 2\sigma_0^2\beta_{l^2}}}$$

If available step lengths were sampled from a log-Normal distribution with tentative mean μ_0 and standard deviation σ_0 , and the log-transformed step length ($\ln[l]$) and its square ($\ln[l]^2$) were included as covariates in the analysis, with resulting coefficient estimates $\beta_{\ln[l]}$ and $\beta_{\ln[l]^2}$ (respectively), the adjusted (selection-free) step length log-Normal mean and standard-deviation parameters are given by:

$$\begin{cases} \hat{\mu} = \frac{(\mu_0 - \sigma_0\beta_{\ln[l]})}{(1 - 2\sigma_0^2\beta_{\ln[l]^2})} \\ \hat{\sigma} = \frac{\sigma_0}{\sqrt{1 - 2\sigma_0^2\beta_{\ln[l]^2}}} \end{cases}$$

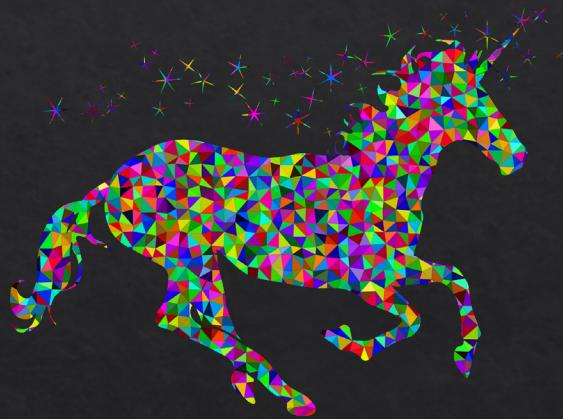
If available step lengths were sampled from a gamma distribution with tentative shape k_0 and scale q_0 , and the step length (l) and its log-transform ($\ln[l]$) were included as covariates in the analysis, with resulting coefficient estimates β_l and $\beta_{\ln[l]}$ (respectively), the adjusted (selection-free) step length gamma shape and scale parameters are given by:

$$\begin{cases} \hat{k} = k_0 + \beta_{\ln[l]} \\ \hat{q} = \frac{1}{\left(\frac{1}{q_0} - \beta_l\right)} \end{cases}$$

If available turn angles were sampled from von Mises distribution with tentative concentration parameter v_0 , and the cosine of the turn angle ($\cos[\theta]$) was included as a covariate in the analysis, with resulting coefficient estimate $\beta_{\cos[\theta]}$, the adjusted (selection-free) von Mises concentration parameter is given by:

$$\hat{v} = v_0 + \beta_{\cos[\theta]}$$

it's R time!



https://github.com/jmsigner/movement_workshop_spring_2023

We have a model – now what?

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- ❖ Interpretation
- ❖ Prediction (mapping)

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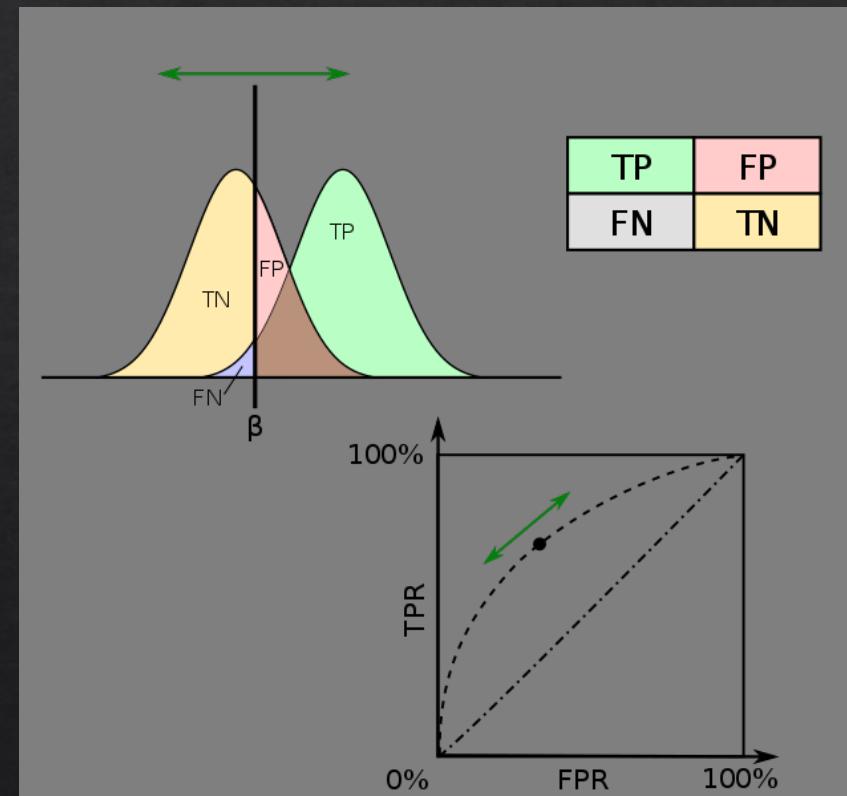
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 - ❖ p-values, standard errors, AIC, likelihood ratio
 - ❖ pseudo R^2
 - ❖ $1 + \frac{\ln(L_M)}{\ln(L_0)}$
 - ❖ what is the appropriate null model?

We have a model – now what?

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 - ❖ p-values, standard errors, AIC, likelihood ratio
 - ❖ pseudo R^2
 - ❖ discrimination indices: ROC-AUC or Concordance
 - ❖ the probability that $w(\text{used}) > w(\text{available})$
 - ❖ what are FN and TN in the context of ‘used-available design’?



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 - ❖ discrimination indices
 - ❖ *Boyce index*: the rank correlation between binned use (observed) and relative intensity (predicted). Requires aggregating data into bins (results are sensitive to the binning procedure)
 - ❖ equal-area bins (geographical space)
 - ❖ equal-count bins (geographical space)
 - ❖ equal-interval bins (environmental space)

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Fieberg, J.R., Forester, J.D., Street, G.M., Johnson, D.H., ArchMiller, A.A. and Matthiopoulos, J. (2018), Used-habitat calibration plots: a new procedure for validating species distribution, resource selection, and step-selection models. *Ecography*, 41: 737-752

Used-habitat calibration plots

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https://cran.r-project.org/web/packages/amt/vignettes/p6_uhc_plots.html

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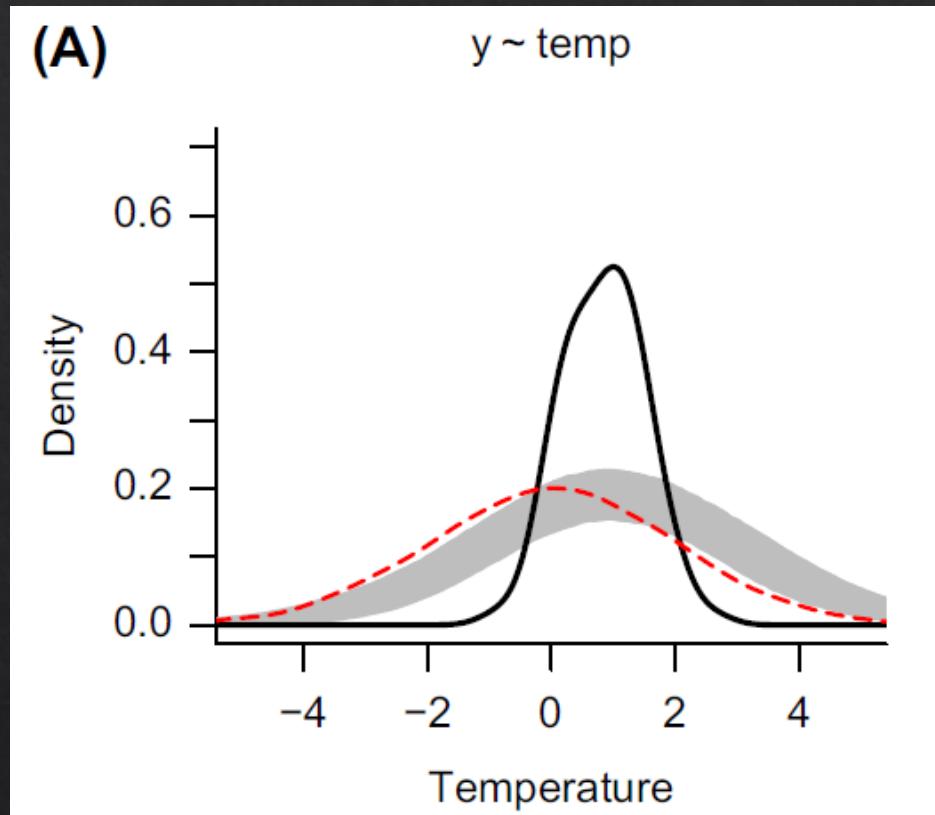
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4. Repeat 1-3 many times
5. Contrast the resulting predicted-use plots with the observed-used plot (produced using the n 'observed-used points'), as well as the 'available plot'

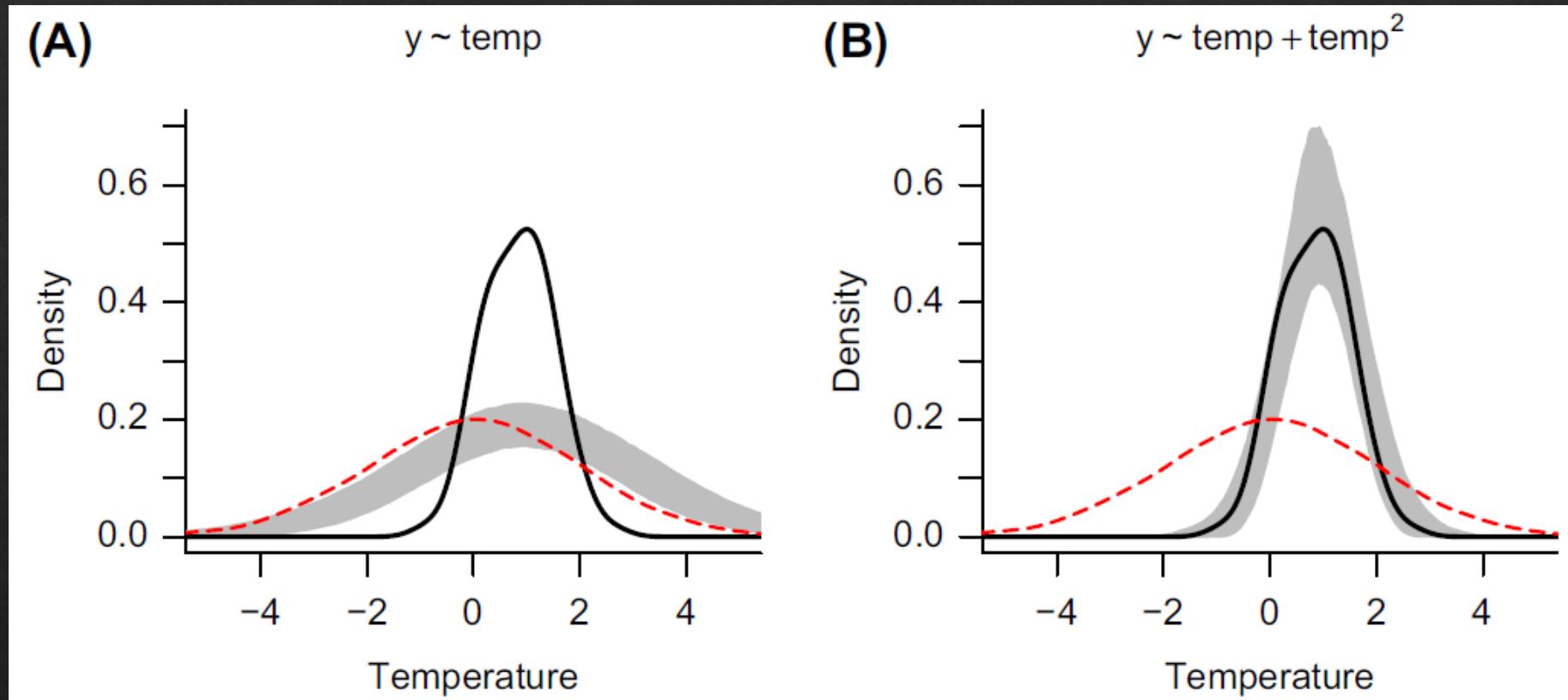
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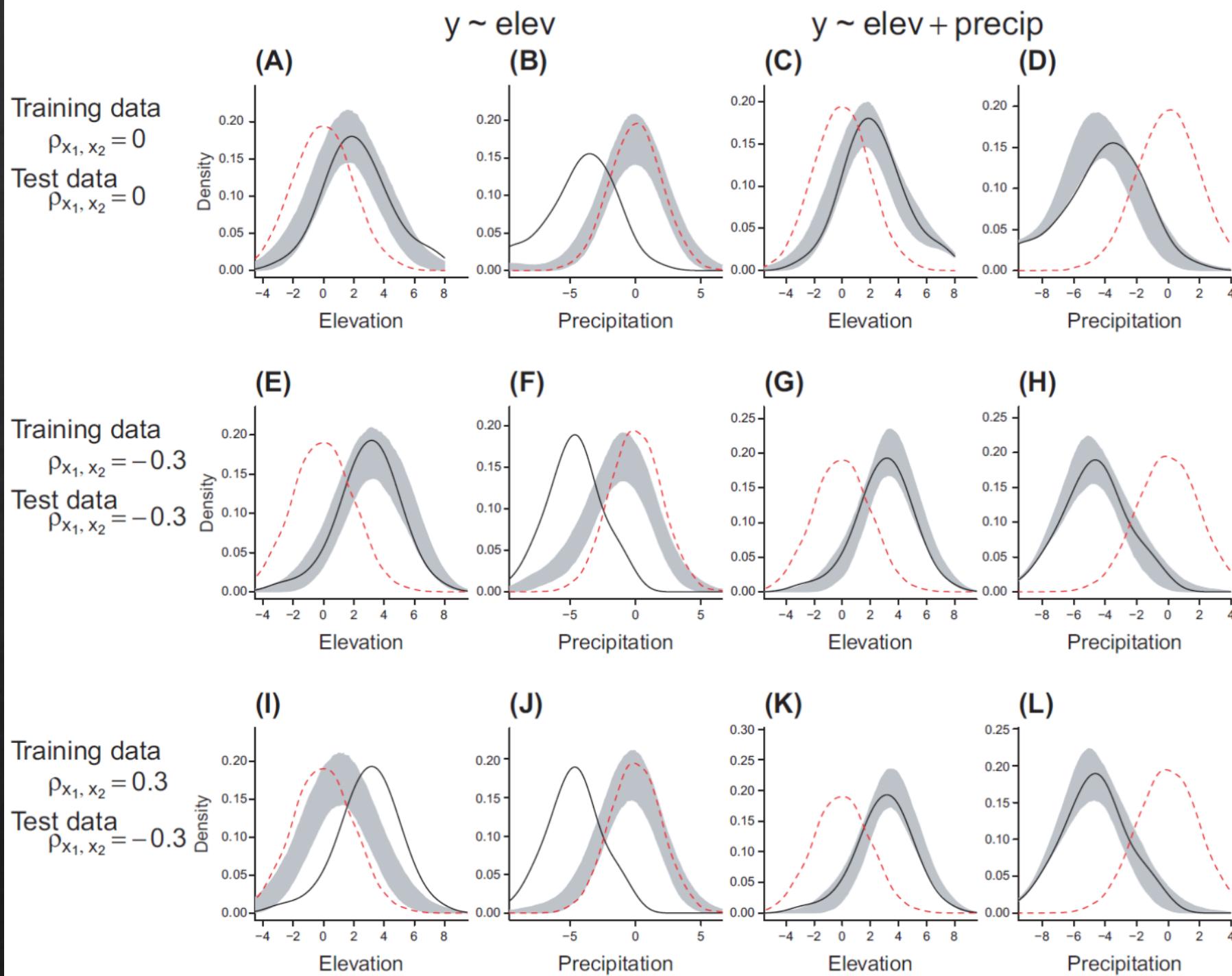


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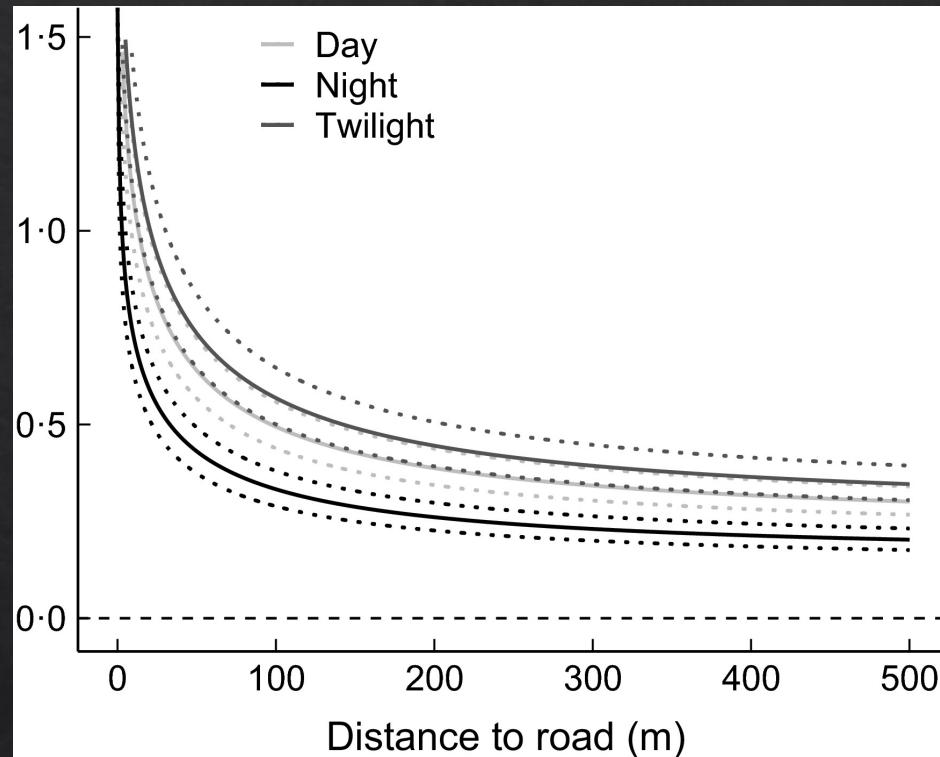
RSS is the relative intensity of use of two equally available habitat units belonging to different sectors of environmental space (categorical), or that differ by one unit along one environmental dimension (continuous)

The natural logarithm of the relative selection strength (logRSS) for location x_1 relative to location x_2 :

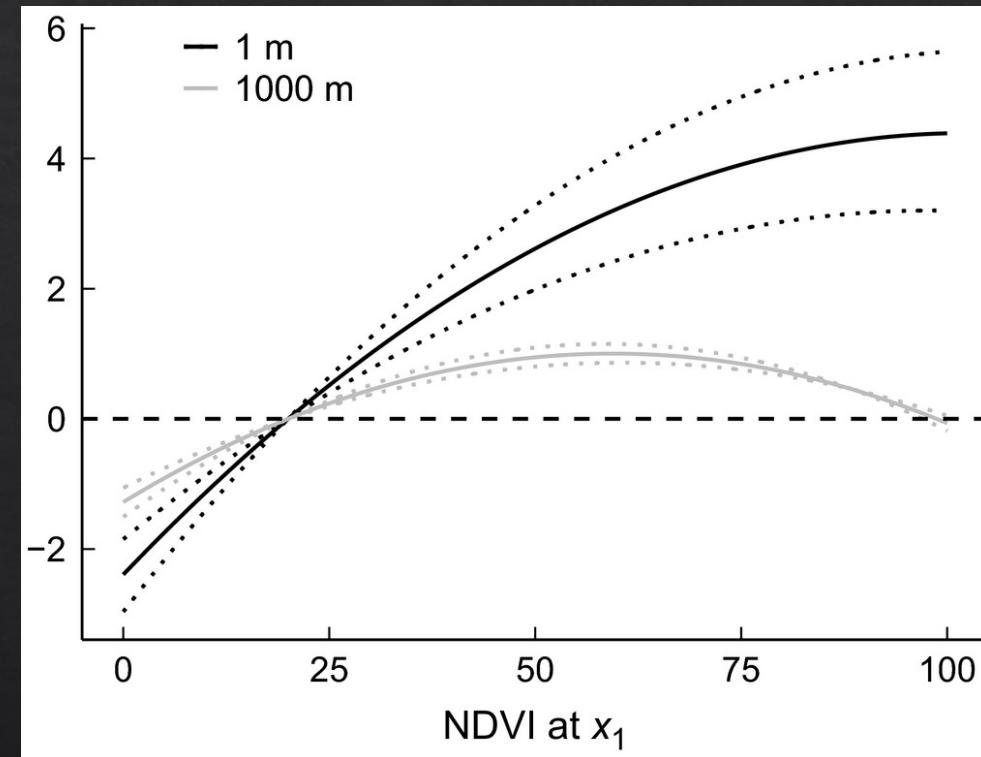
$$\ln \left[\frac{\exp(\sum_{j=1}^m [\beta_j \cdot h_j(x_1)])}{\exp(\sum_{j=1}^m [\beta_j \cdot h_j(x_2)])} \right] = \sum_{j=1}^m (\beta_j \cdot [h_j(x_1) - h_j(x_2)])$$

The selection coefficient for habitat covariate j , β_j , is logRSS for x_1 vs x_2 , conditional on $[h_j(x_1) - h_j(x_2)] = 1$ and all other covariates being equal; β_j is the ‘conditional effect size’ of h_j

Relative Selection Strength (RSS)



$\ln(RSS)$ for selecting location x_1 over x_2 as function of the distance from the road at x_1 and where x_2 is always 250 m further away from the road



$\ln(RSS)$ for selecting location x_1 over x_2 where $\text{NDVI}(x_2) = 20$ and x_1 and x_2 are equidistance from a road (either 1 m or 1000 m)

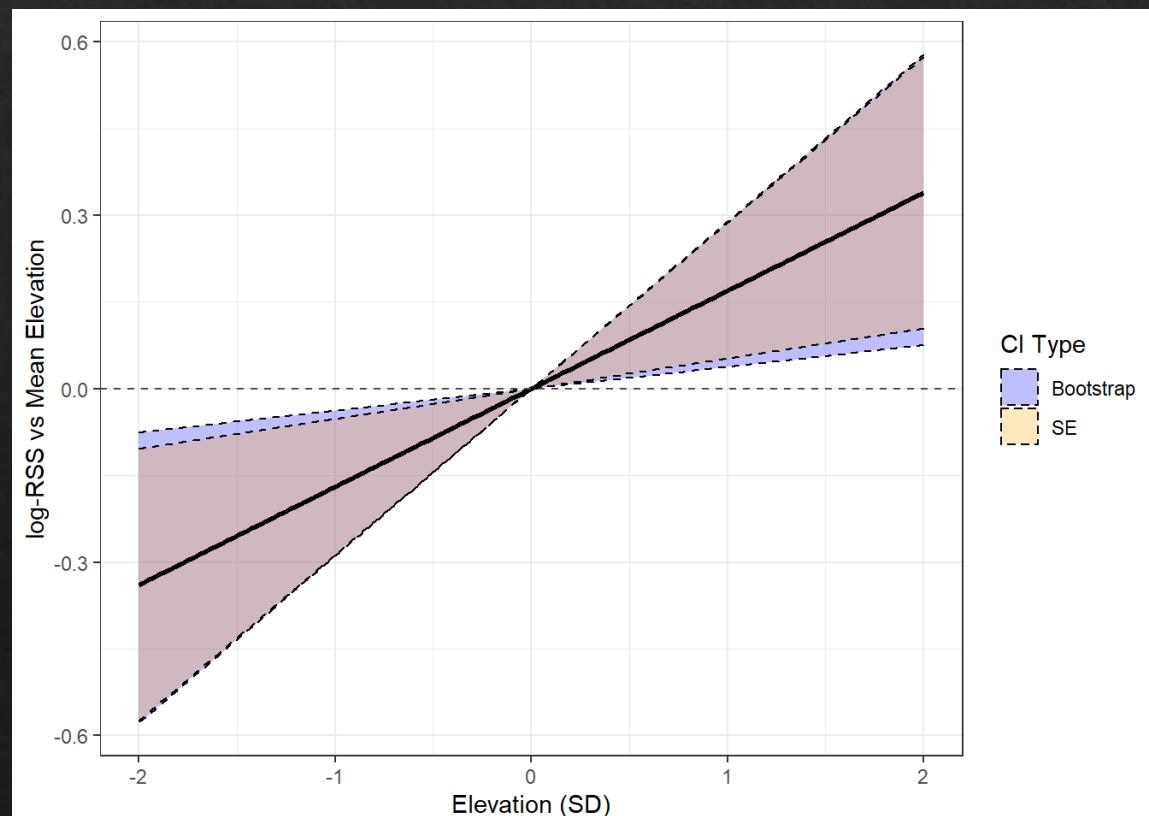
We have a model – now what?

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- ❖ Interpretation: Relative Selection Strength (RSS)
 - ❖ RSS uncertainty

Fieberg, J., Signer, J., Smith, B., & Avgar, T. (2021). A "How to" guide for interpreting parameters in habitat-selection analyses. Journal of Animal Ecology, 90(5), 1027-1043

https://bsmity13.github.io/log_rss/

https://github.com/jmsigner/movement_workshop_spring_2023



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If we used a Binomial GLM to fit the eHSF,
we should predict on the link-scale and then exponentiate
(rather than predict on the response scale)

Predicting space-use from iSSF

Do not apply the iSSF to a raster; simulate!

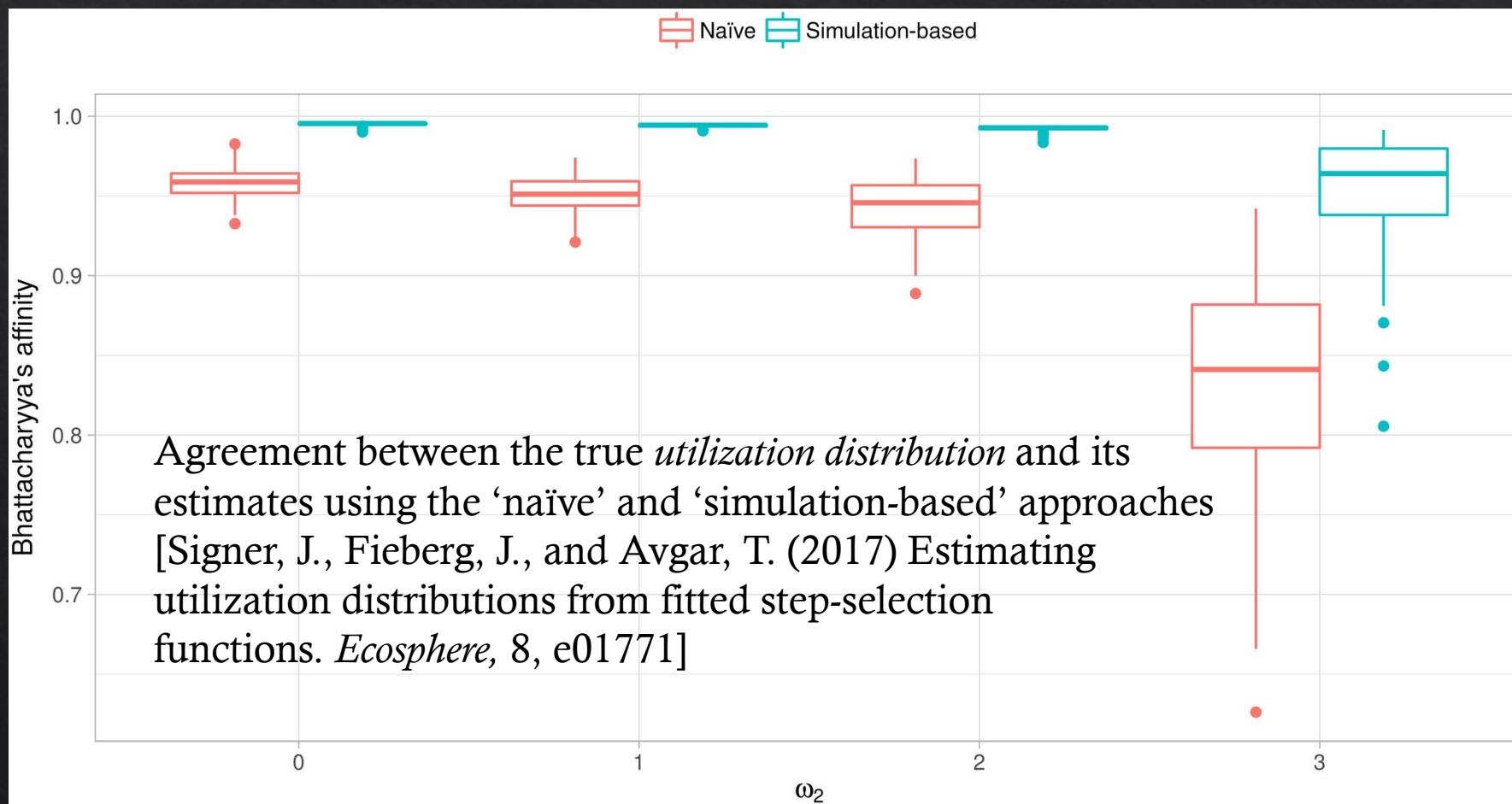
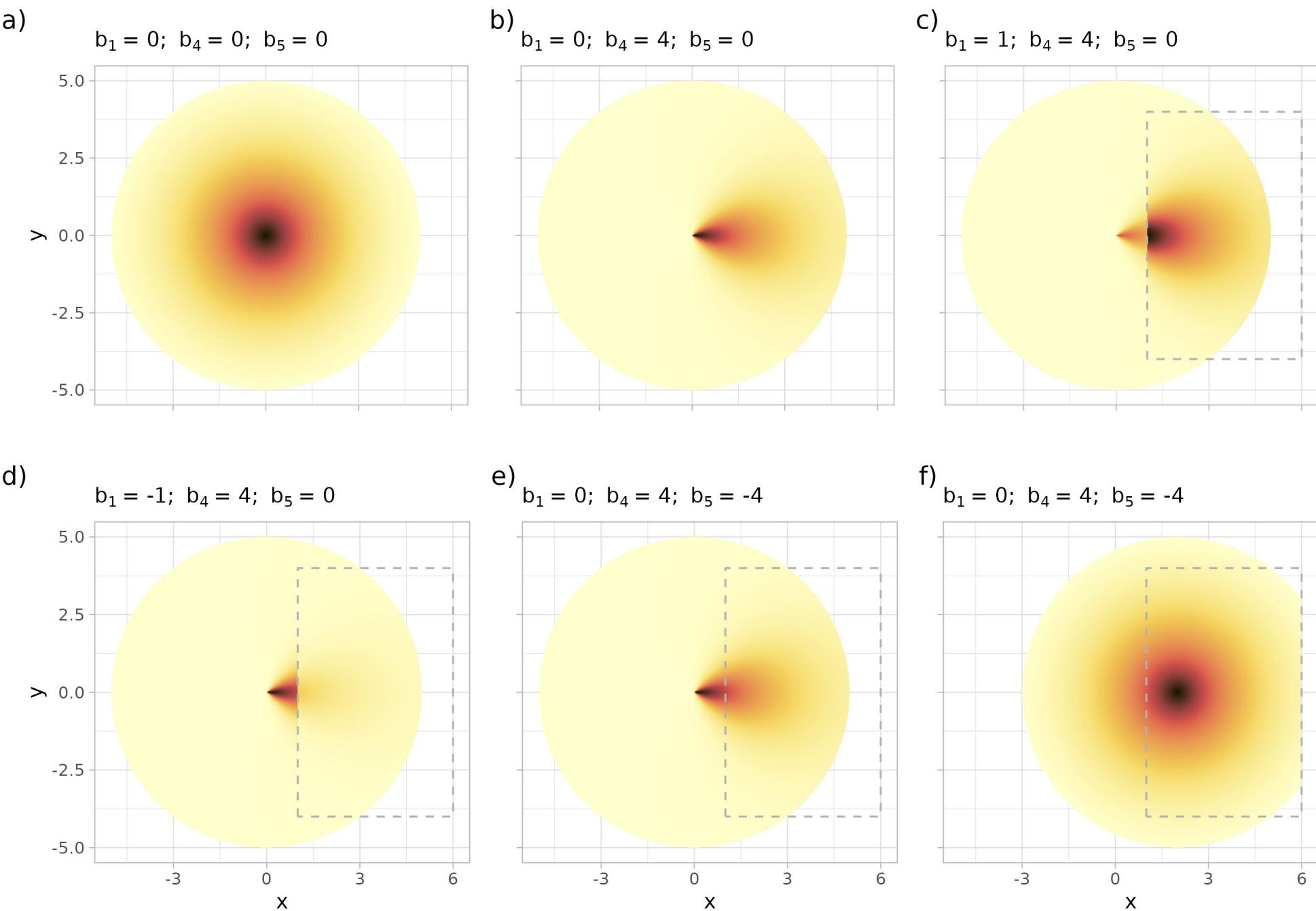
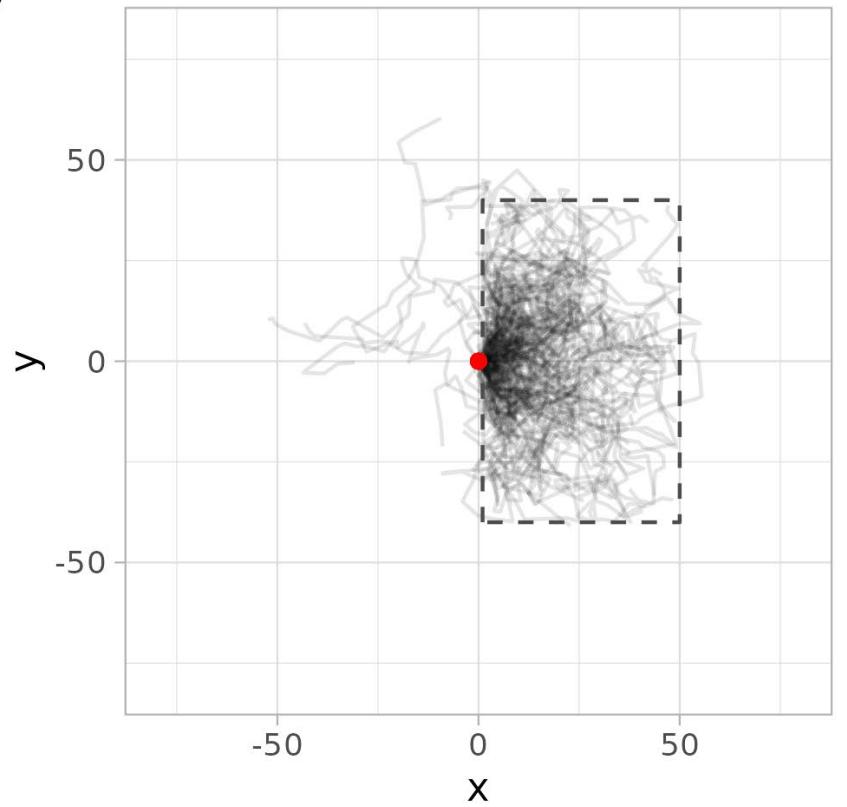


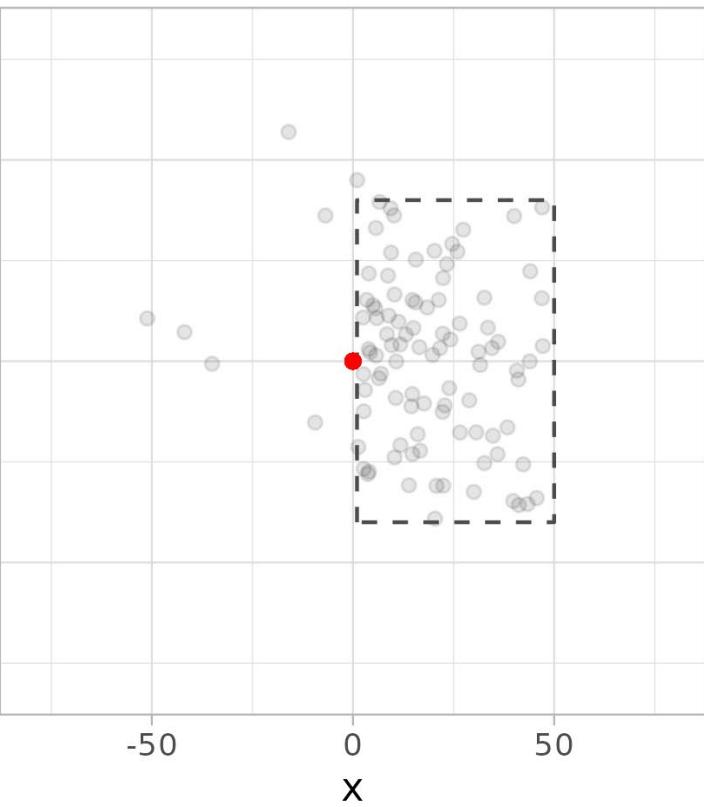
Figure 1: Different redistribution kernels resulting from different parametrizations of the selection-free movement kernel (SF-MK) and the movement-free habitat selection function (MF-HSF). In the simplest case, there is no habitat selection and movement is only constrained by the SF-MK, which excludes (panel a) or includes (panel b) directional persistence. An environmental covariate (gray rectangle within which $h = 1$, as opposed to out of the rectangle where $h = 0$) can lead to preference (panel c) or avoidance (panel d). Furthermore, the SF MK can also depend on the habitat the animal is in at the start of the movement step. We show redistribution kernels for a case where the animal exhibits different directional persistence depending on whether it is located outside (panel e) or inside (panel f) the gray rectangle.



a)



b)



c)

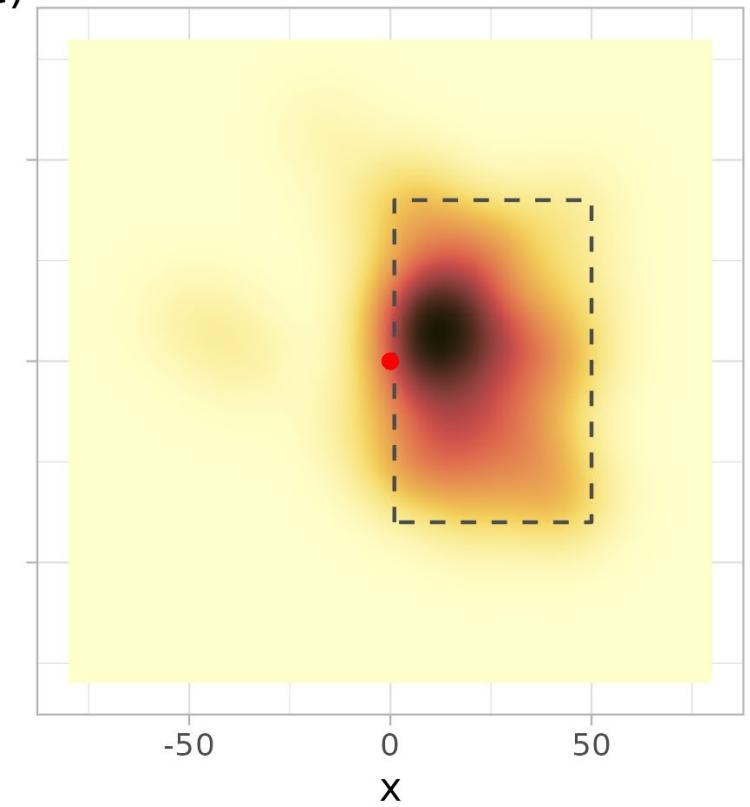


Figure 2: Simulated movement paths of 50 animals for 30 time steps (panel a). We then used the end positions (panel b) to generate a smoothed map representing the transient Utilization Distribution at $t = 30$ (panel c). The start point is marked with a red dot.



https://github.com/jmsigner/movement_workshop_spring_2023

Environmental-Variable Transformation

Why?

- ❖ to facilitate model convergence
- ❖ to allow comparing effect sizes
- ❖ to enhance interpretability and biological realism

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- ❖ scaling (divide by sd with or without subtracting the mean)
- ❖ normalizing (0-1)
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What's the Question?



Dealing with Structured Data

- ❖ Datasets are often structured, meaning they include multiple data folds
 - ❖ Individuals
 - ❖ Populations
 - ❖ Study areas or periods



<https://susanbrack.com/home.html>

Dealing with Structured Data

- ❖ Datasets are often structured, meaning they include multiple data folds
 - ❖ Individuals
 - ❖ Populations
 - ❖ Study areas or periods
- ❖ Within-fold variance is generally smaller than between-fold variance
 - ❖ Violation of *iid* assumptions
 - ❖ Population-level (rather than fold-specific) inference is typically the goal



<https://susanbrack.com/home.html>

Dealing with Structured Data

1. Balance the sample size across folds
 - a) Thin data-rich folds and/or resample data (with replacement) to increase the sample size for data-poor folds
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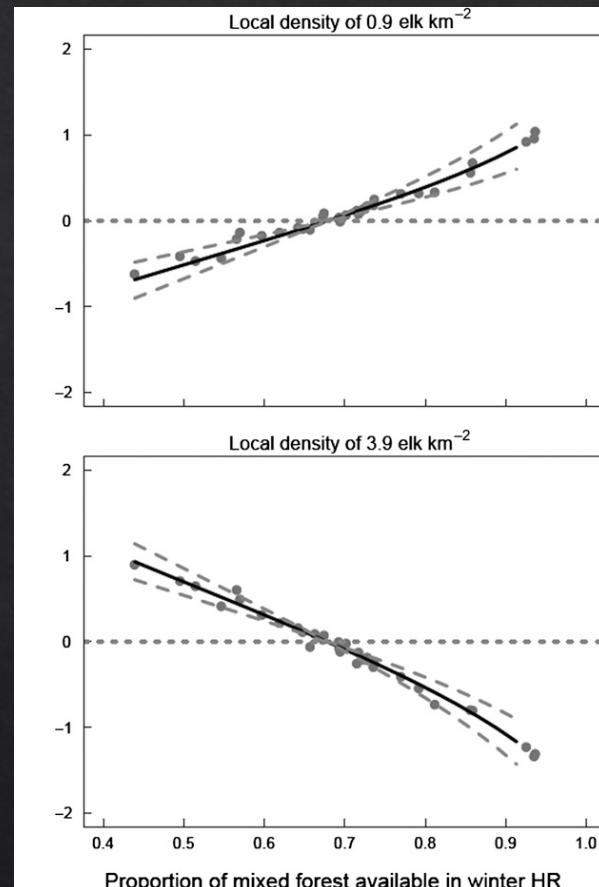
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3. Use a hierarchical (mixed-effects) model
 - a) Use fold-specific random intercepts to fit a population-level eHSF with fold-coupled use-available sets (i.e., whenever availability is different across folds).
 - b) Use fold-specific random slopes to fit a population-level eHSF while allowing selection coefficients to vary amongst folds
 - c) For iSSF, use a mixed-effects Poisson regression [Muff *et al.* 2020]



Dealing with Density or Availability Dependence

Habitat-selection patterns vary with habitat availability and population density



Matthiopoulos, J., Hebblewhite, M., Aarts, G. and Fieberg, J. (2011), Generalized functional responses for species distributions. *Ecology*, 92: 583-589.

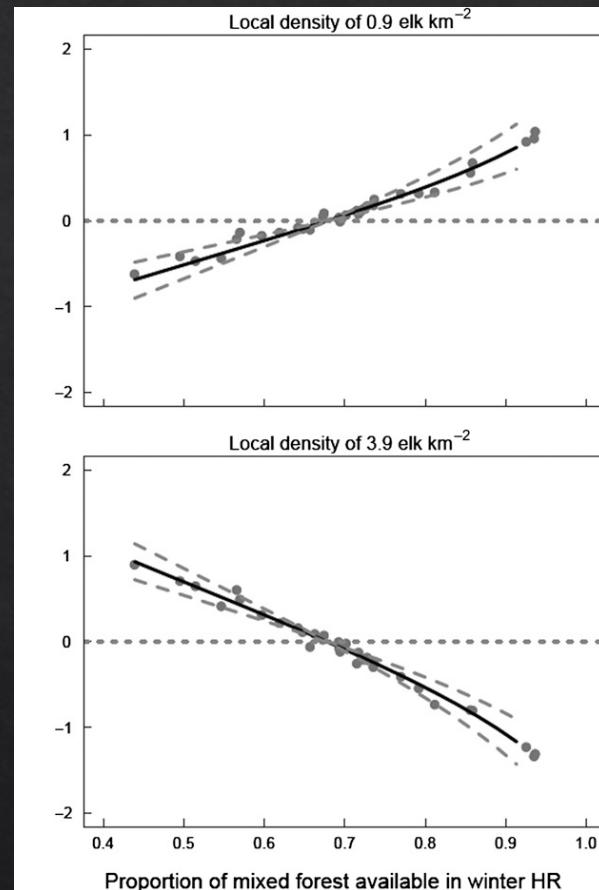
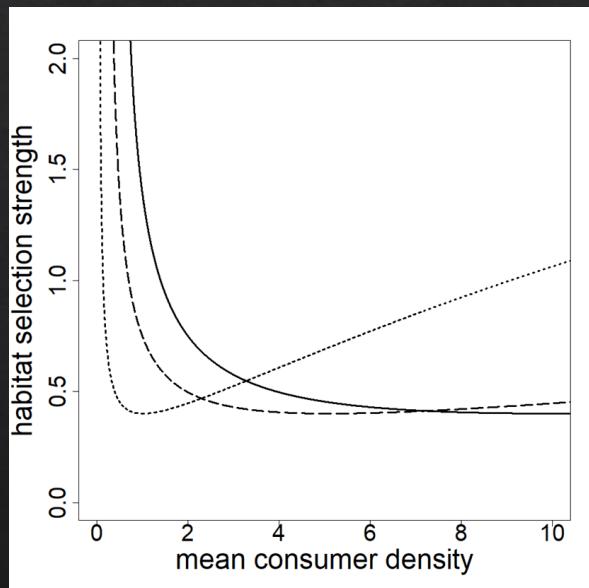
van Beest, F.M., McLoughlin, P.D., Mysterud, A. and Brook, R.K. (2016), Functional responses in habitat selection are density dependent in a large herbivore. *Ecography*, 39: 515-523.

Avgar, T., Betini, GS, Fryxell, JM. (2020) Habitat selection patterns are density dependent under the ideal free distribution. *J Anim Ecol*. 89: 2777–2787

Smith, B.J., MacNulty, D.R., Stahler, D.R., Smith, D.W. & Avgar, T. (2023) Density-dependent habitat selection alters drivers of population distribution in northern Yellowstone elk. *Ecology Letters*, 26, 245–256.

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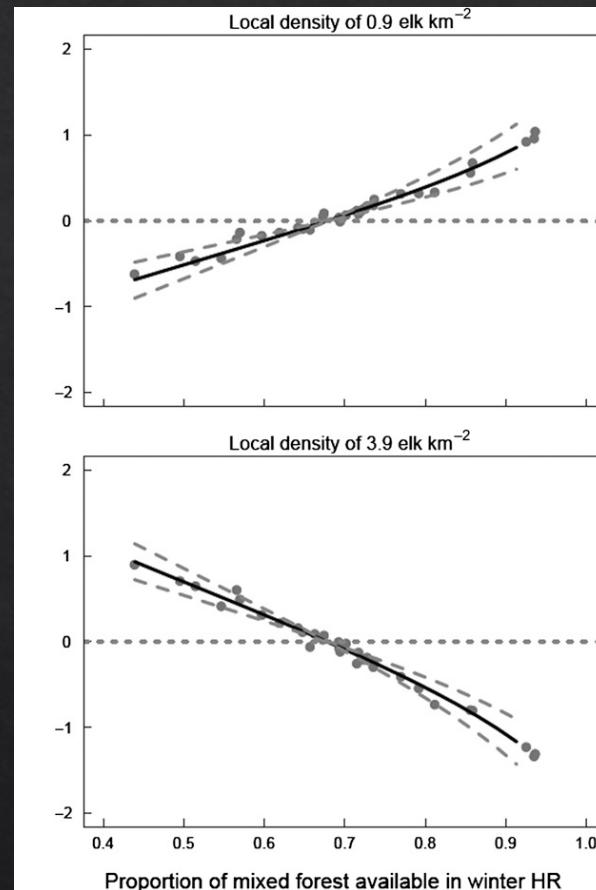
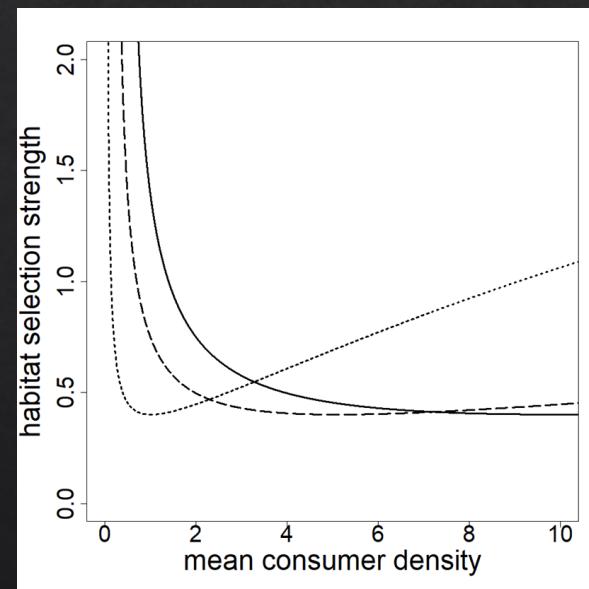
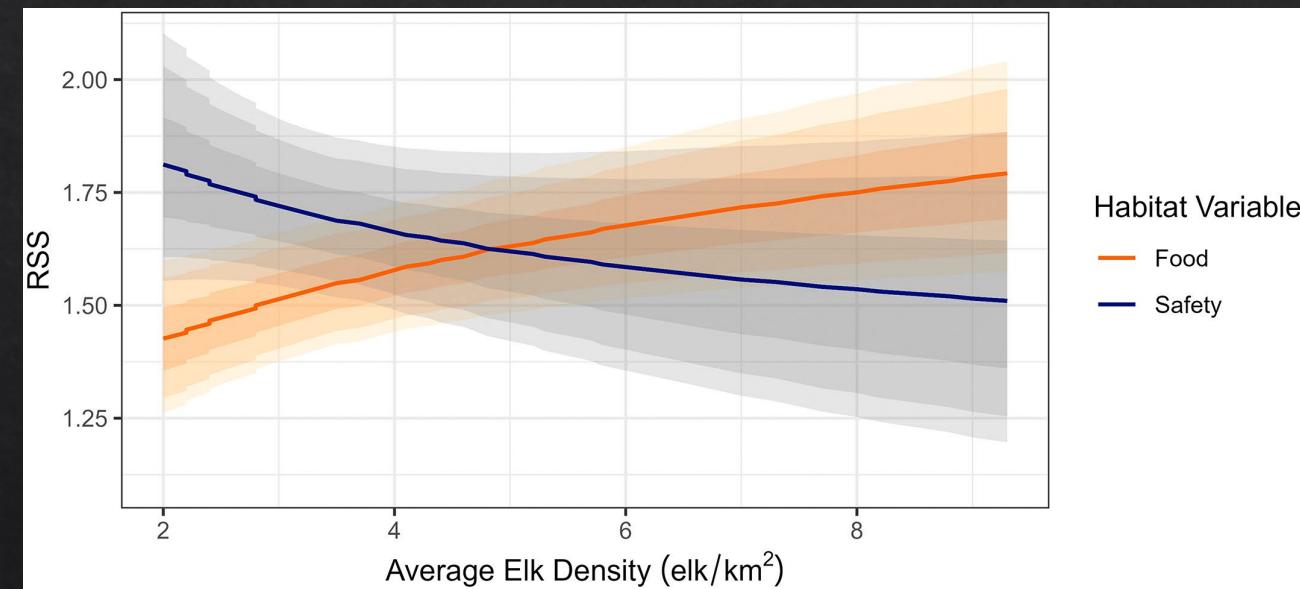
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Dealing with Density or Availability Dependence

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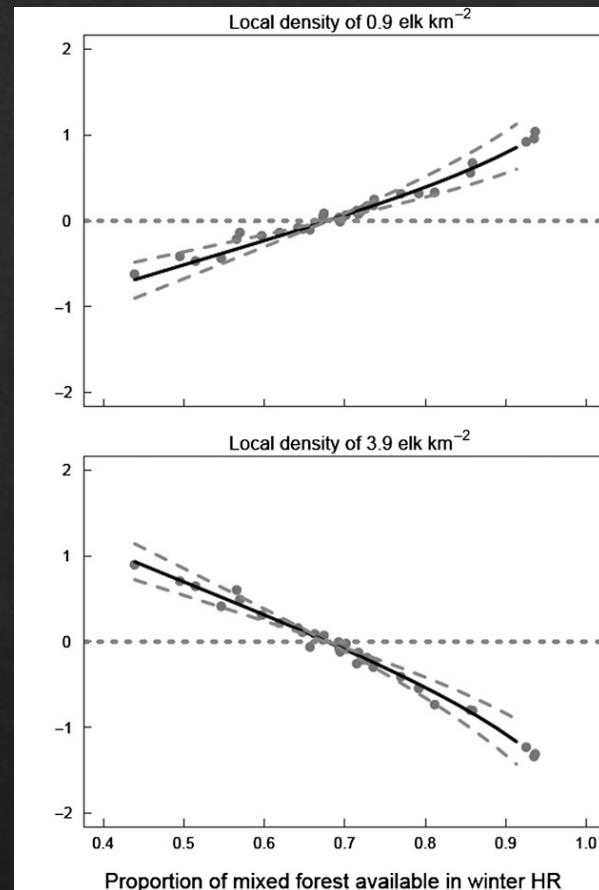
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Dealing with Density or Availability Dependence

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- After fitting an individual model to each fold (while conserving model structure across folds), examine relationship between fold-specific coefficient estimates for a given variable and fold-specific population density and/or variable availability



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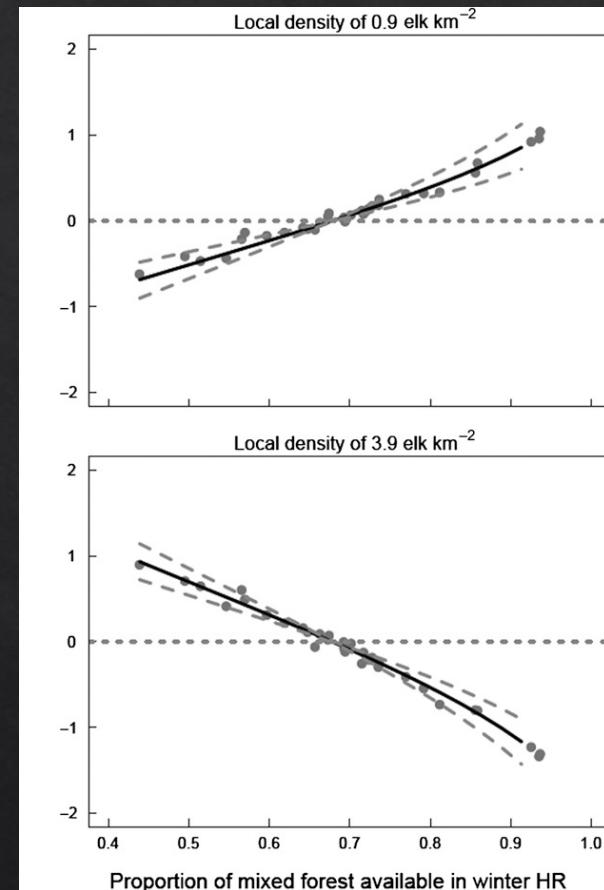
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Habitat-selection patterns vary with habitat availability and population density

- After fitting an individual model to each fold (while conserving model structure across folds), examine relationship between fold-specific coefficient estimates for a given variable and fold-specific population density and/or variable availability
- Fit a single model while including interactions between habitat variables and fold and/or cluster (for iSSF) specific population density and/or variable availability



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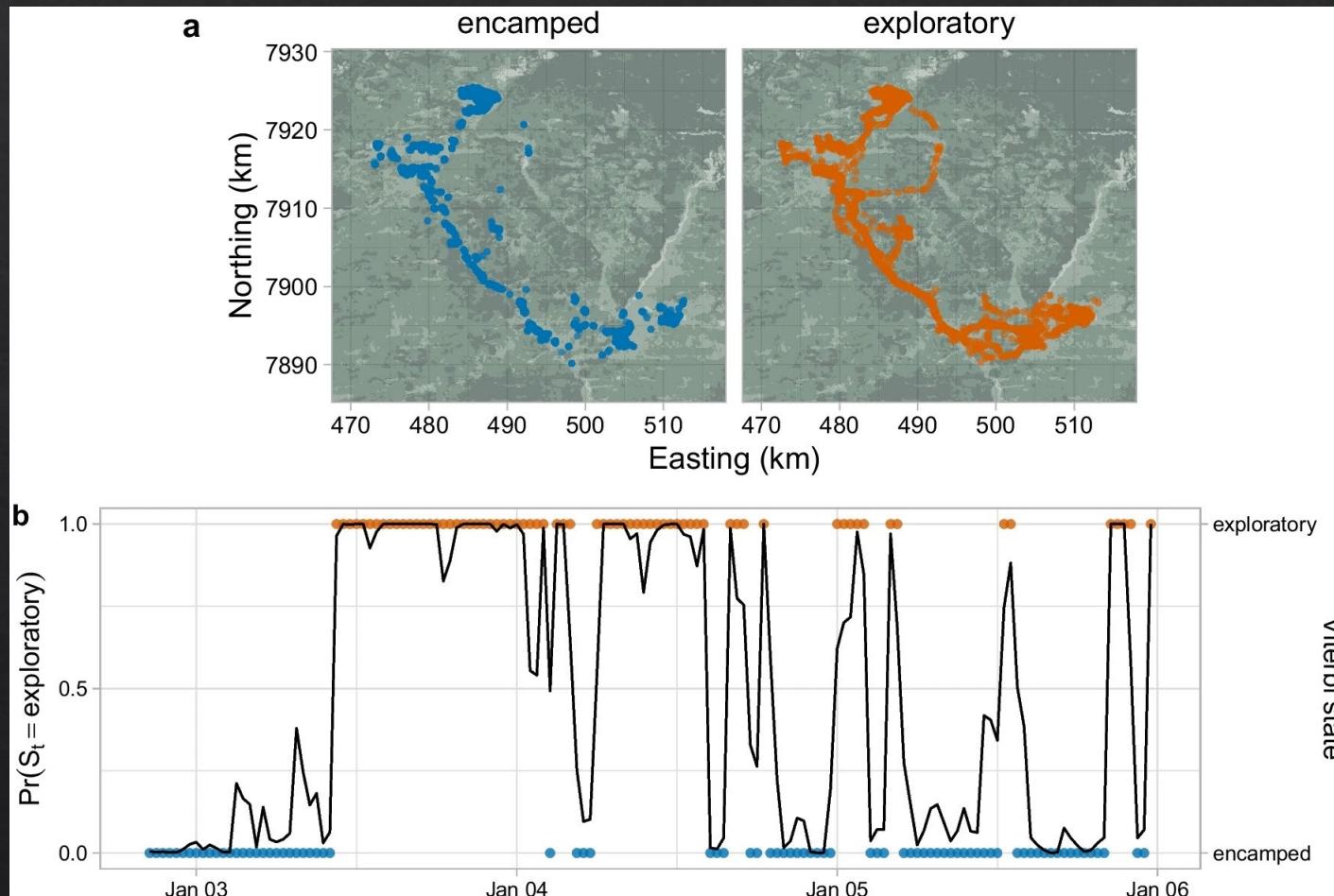
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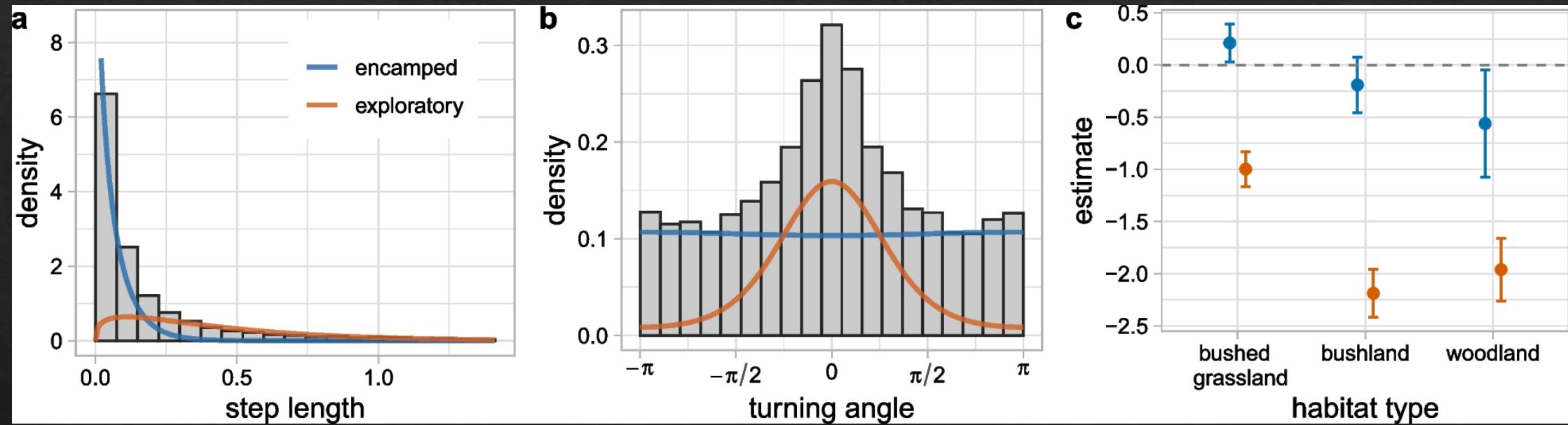
Dealing with Behavioral-State Dynamics in iSSF



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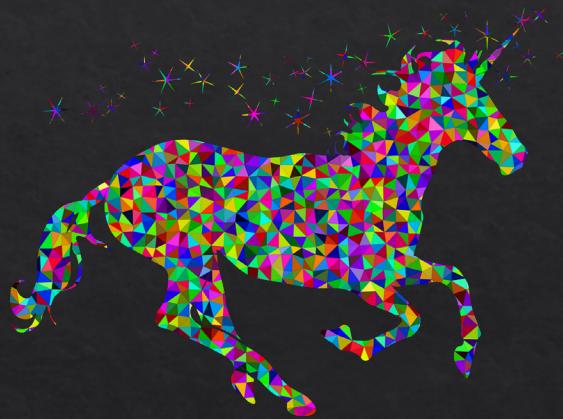
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it's R time!



https://github.com/jmsigner/movement_workshop_spring_2023