Step Selection Functions
A brief Introduction

AfriMove Meeting

2025-05-22

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Agenda

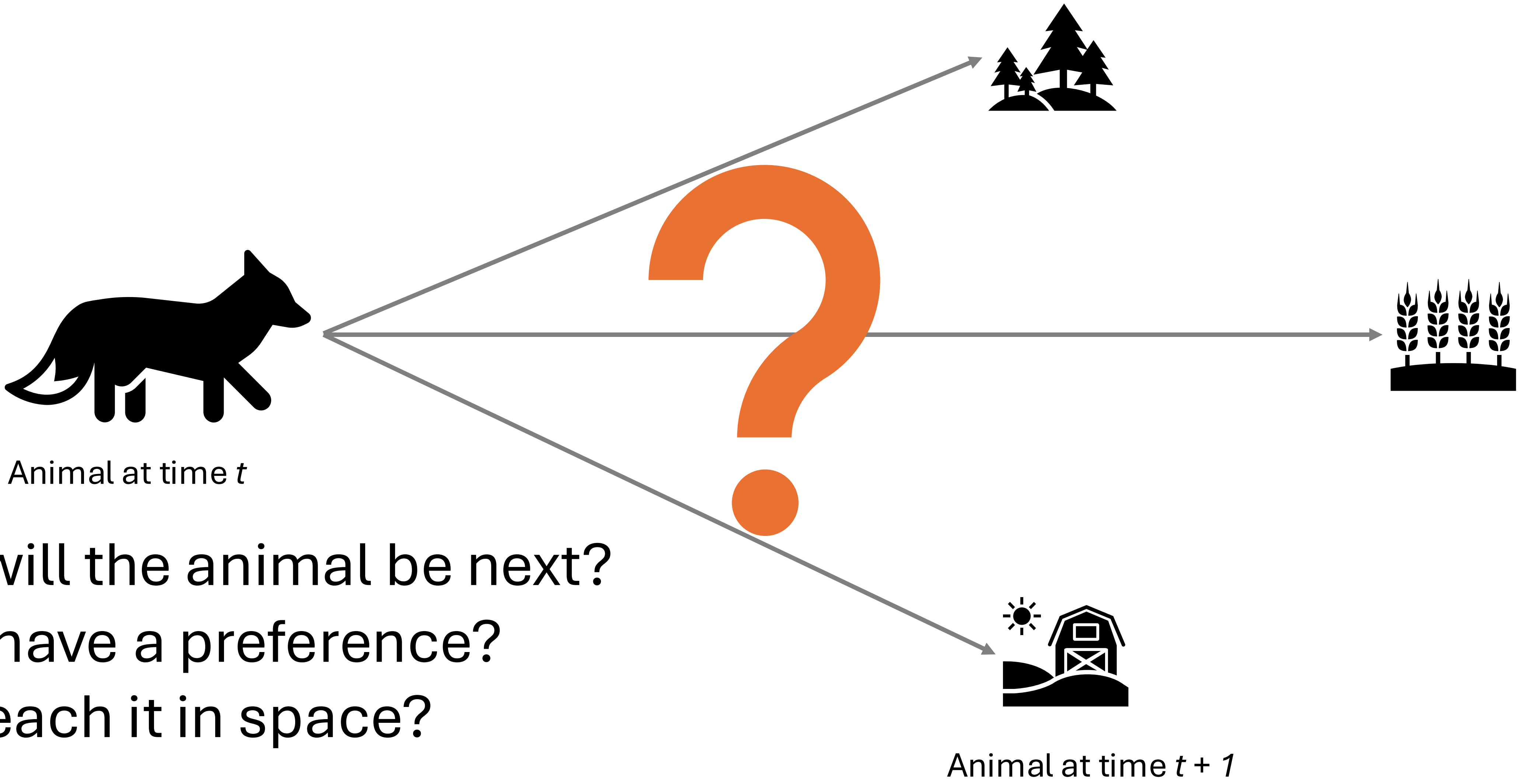
- Some background about SSF
- A practical example of red deer from northern Germany

- Slides, data and coded examples are available here: https://github.com/jmsigner/2025_afrimove_talk

Who am I?

- Research in Wildlife Science (University of Göttingen, German; Group of Niko Balkenhol).
- Interest in statistical ecology, particularly in the analysis of telemetry data.
- Involved in SASSCAL Antelope project.

What is it all about?

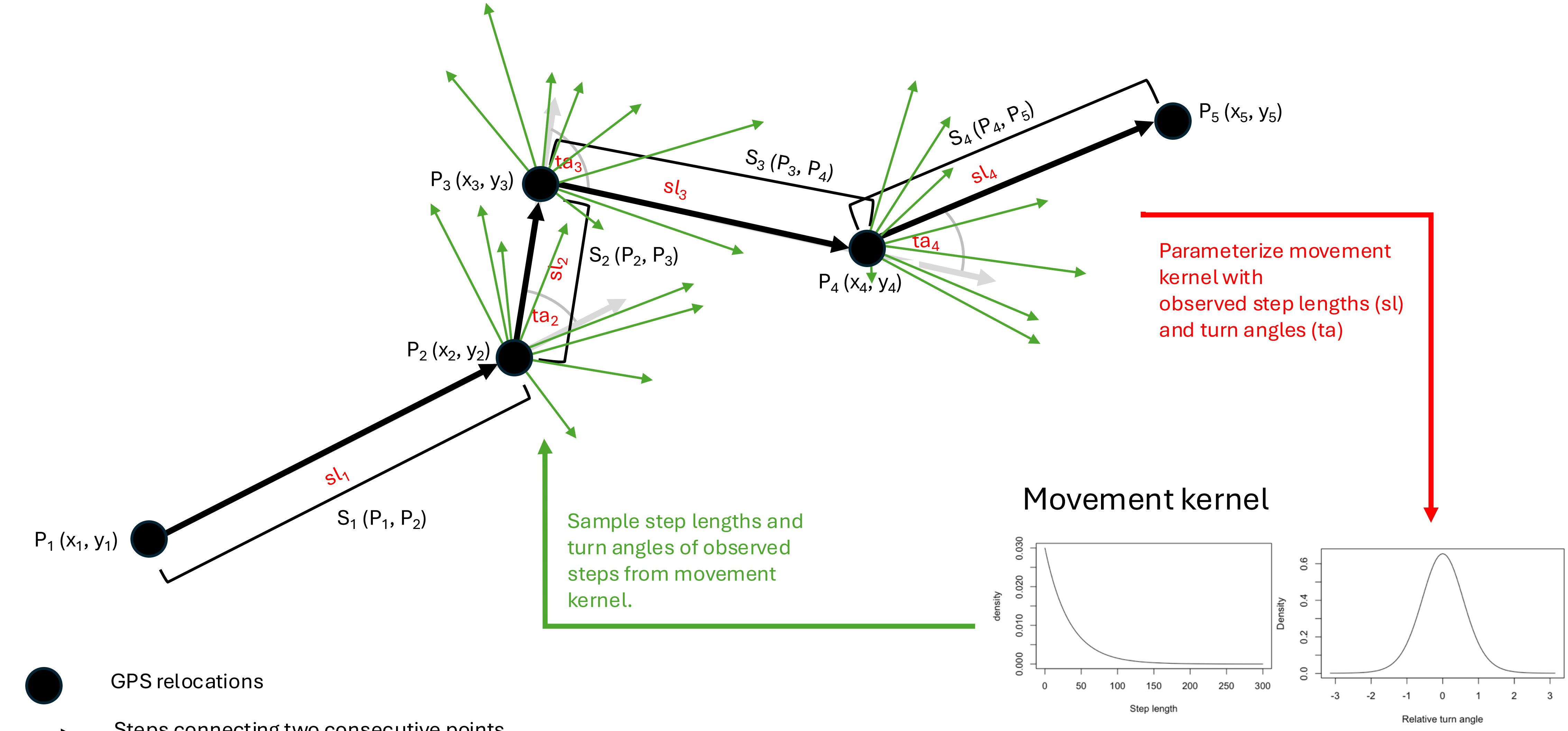


Where will the animal be next?
Does it have a preference?
Can it reach it in space?

What is the difference:

- Resource Selection Function (RSF; also sometimes referred to as Habitat Selection Function; HSF): **Global availability**, i.e., the animal assumed to reach each available point at each time step.
- Step Selection Functions (SSF): **Conditional availability**, available steps are conditioned on the current position of the animal.
- Integrated Step Selection Function (iSSF): **Conditional availability** and also estimating a movement kernel, i.e., where to expect the animal in the next time step, if there were no selection.

SSF the idea



Step length distribution: usually exponential or gamma.

Turn angle distribution: usually von Mises.

Next steps

- Extract covariate values at the end (habitat selection) or start (movement kernel) of random and observed steps
- Estimate selection coefficients with using a conditional logistic regression (other frameworks can be used).
- Work with the results

Adding movement to Habitat Selection

- Avgar 2015 showed, that we can (and in fact) should disentangle habitat selection and movement.

BRITISH ECOLOGICAL SOCIETY | Methods in Ecology and Evolution

Standard Paper | Open Access

Integrated step selection analysis: bridging the gap between resource selection and animal movement

Correction(s) for this article

Tal Avgar, Jonathan R. Potts, Mark A. Lewis, Mark S. Boyce

First published: 15 December 2015 | https://doi.org/10.1111/2041-210X.12528 | Citations: 348

Implementation of an iSSF

- iSSFs are not hard, but some steps (especially data preparation can be tedious).
- **amt** was designed to make this step easier.
- Strong dependency on other R packages to perform geospatial analysis (e.g., **sf**, **terra**).

Ecology and Evolution

Forward Series

ORIGINAL RESEARCH | Open Access

Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses

Johannes Signer, John Fieberg, Tal Avgar

First published: 05 February 2019 | https://doi.org/10.1002/ece3.4823 | Citations: 431

Typical workflow

- Load data (here we use data from the amt package)
- Make a track (amt data format)
- *Optionally, regularize the track (for regular sampling intervals).*
- Create steps
- Create random steps
- Extract covariates
- Annotate time of day

```
data(deer)

dat1 <-
  deer |>
  steps() |>
  random_steps() |>
  extract_covariates(dist_forest) |>
  time_of_day()
```

This yields the following data

```
> head(dat1)
# A tibble: 6 × 13
       x1_      x2_      y1_      y2_     sl_    ta_ t1_                 t2_                 dt_          case_ step_id_ dist_forest tod_end_
*    <dbl>    <dbl>    <dbl>    <dbl>   <dbl>  <dbl> <dttm>              <dttm>              <drtn>       <lgl>    <dbl>       <dbl> <fct>
1 4314053. 4314105. 3445768. 3445859. 104.     3.00  2008-03-30 06:00:54 2008-03-30 12:01:47 6.014722 … TRUE         3      -0.398 day
2 4314053. 4314053. 3445768. 3445768.   0.149 -0.218 2008-03-30 06:00:54 2008-03-30 12:01:47 6.014722 … FALSE        3      -0.787 day
3 4314053. 4314299. 3445768. 3445243. 580.     0.819 2008-03-30 06:00:54 2008-03-30 12:01:47 6.014722 … FALSE        3       0.119 day
4 4314053. 4314157. 3445768. 3446139. 385.    -3.03  2008-03-30 06:00:54 2008-03-30 12:01:47 6.014722 … FALSE        3       0.545 day
5 4314053. 4314175. 3445768. 3445890. 172.     2.74  2008-03-30 06:00:54 2008-03-30 12:01:47 6.014722 … FALSE        3      -0.202 day
6 4314053. 4313506. 3445768. 3446225. 712.    -1.89  2008-03-30 06:00:54 2008-03-30 12:01:47 6.014722 … FALSE        3      -0.398 day
```

Fitting a fist model (m0)

```r
m0 <- fit_clogit(
  case_ ~ # This is the response
    dist_forest + # distance to forest
    strata(step_id_), # each stratum is an observed step with its random steps
  data = dat1, # the data
  model = TRUE # to save the input data
)
```

```
               coef exp(coef) se(coef)      z Pr(>|z|)
dist_forest -1.4222    0.2412   0.1118 -12.72   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

The closer to the forest (negative values) the better.

Relative Selection Strength (RSS)

- The RSS indicates how much more like it is to selection a location x_1 relative to a reference location x_2.

- $RSS(x_2, x_1) = w(x) / w(x1)$

```
> x1 <- data.frame(dist_forest = 1)
> x2 <- data.frame(dist_forest = 0)
> exp(log_rss(m0, x1, x2)$df$log_rss)
[1] 0.2411831
> exp(coef(m0))
dist_forest
  0.2411831
```

Ecology and Evolution

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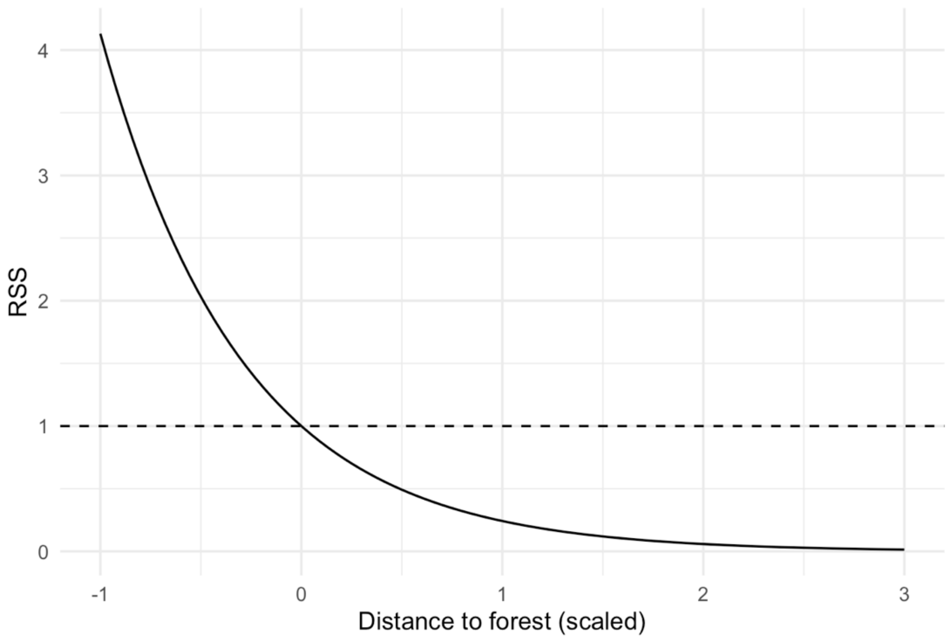
ORIGINAL RESEARCH | Open Access

Relative Selection Strength: Quantifying effect size in habitat- and step-selection inference

Tal Avgar, Subhash R. Lele, Jonah L. Keim, Mark S. Boyce

First published: 14 June 2017 | https://doi.org/10.1002/ece3.3122 | Citations: 151



Let’s add an interaction with time of day

- Maybe, there is different selection behavior for distance to forest during day than during the night?

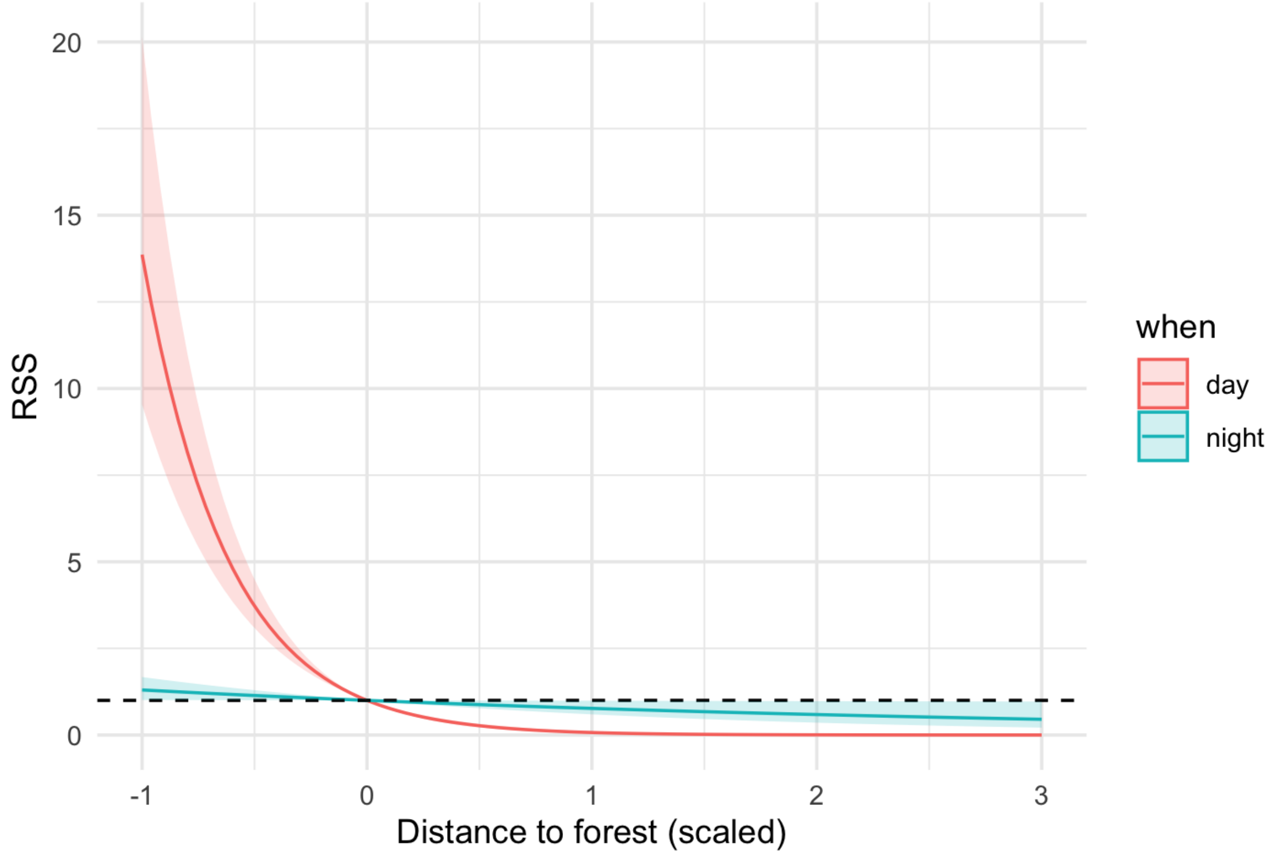
```
m1 <- fit_clogit(
  case_ ~ # This is the response
    dist_forest + # distance to forest
    dist_forest:tod_end_ + # as interaction with time of day
    strata(step_id_), # each stratum is an observed step with its random
steps
  data = dat1, # the data
  model = TRUE # to save the input data
)
```

difference between day and night (2)

```
                              coef exp(coef) se(coef)     z Pr(>|z|)
dist_forest               -2.62923   0.07213  0.19056 -13.8   <2e-16 ***
dist_forest:tod_end_night  2.36636  10.65857  0.22968  10.3   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**'
```

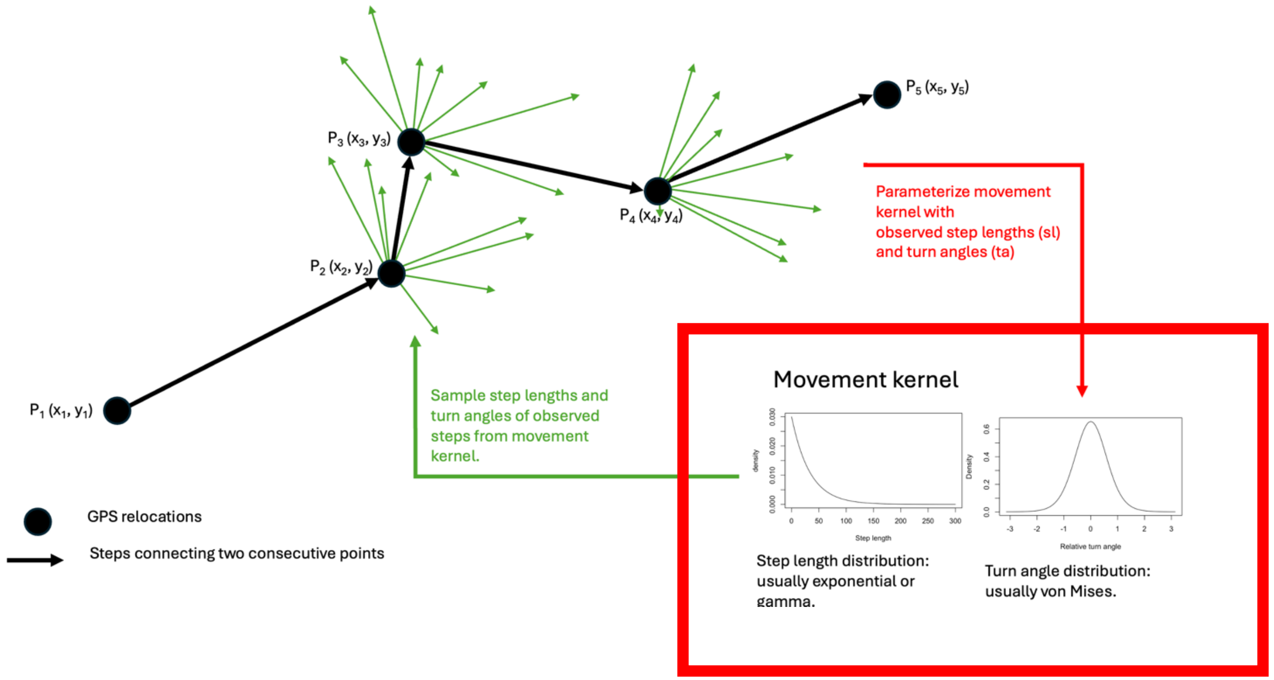
During day: Even stronger selection for forest.

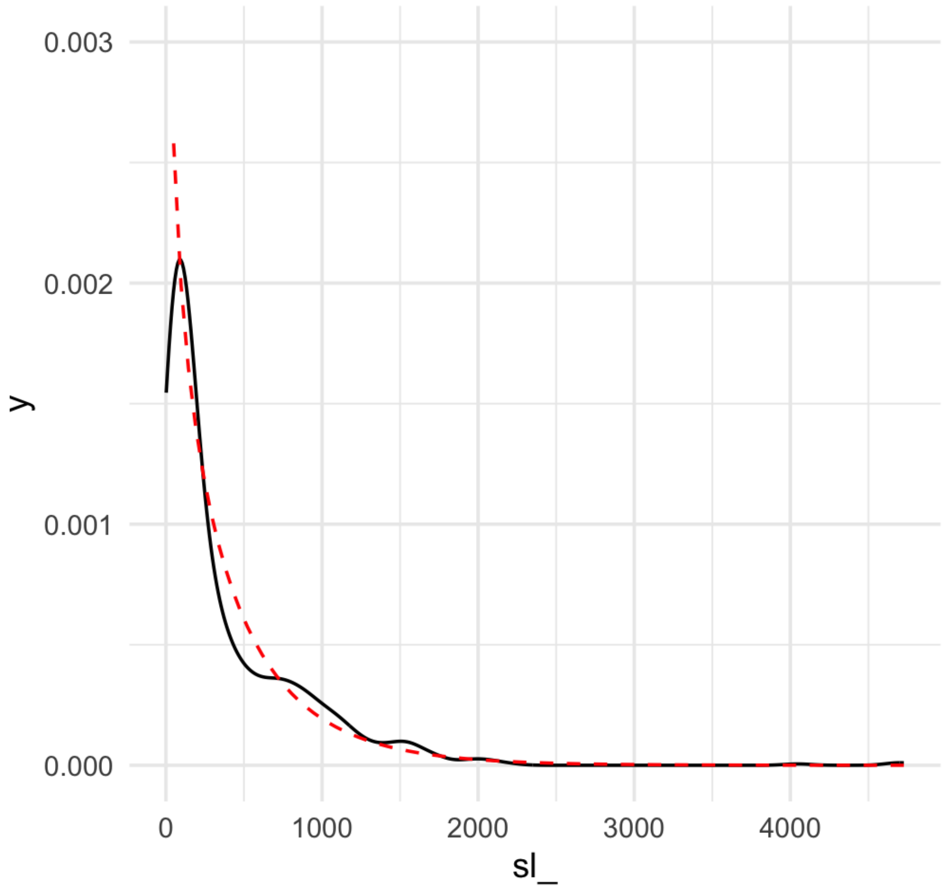
During night?



Include movement: The tentative movement kernel

Step length distribution (shown here) and turn angle distribution estimated from the data





Extending SSF to iSSF

```r
m2 <- fit_clogit(
  case_ ~ # This is the response
    dist_forest + # distance to forest
    dist_forest:tod_end_ + # as interaction with time of day

    # movement model
    sl_ +
    log(sl_) +

    strata(step_id_), # each stratum is an observed step with its random steps
  data = dat1, # the data
  model = TRUE # to save the input data
)
```

We use a Gamma distribution to model step lengths: sl_ links to the shape and log(sl_) to the scale parameter.

```
                               coef  exp(coef)   se(coef)       z  Pr(>|z|)
dist_forest              -2.6255942  0.0723967  0.1879899 -13.967   <2e-16 ***
sl_                       0.0001785  1.0001785  0.0001249   1.429    0.153
log(sl_)                  0.0497895  1.0510498  0.0360540   1.381    0.167
dist_forest:tod_end_night 2.2453567  9.4437832  0.2289693   9.806   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Linking estimated coefficients to tentative distributions

BRITISH ECOLOGICAL SOCIETY Journal of Animal Ecology

A ‘How to’ guide for interpreting parameters in habitat-selection analyses

John Fieberg, Johannes Signer, Brian Smith, Tal Avgar

First published: 14 February 2021 | https://doi.org/10.1111/1365-2656.13441 | Citations: 177

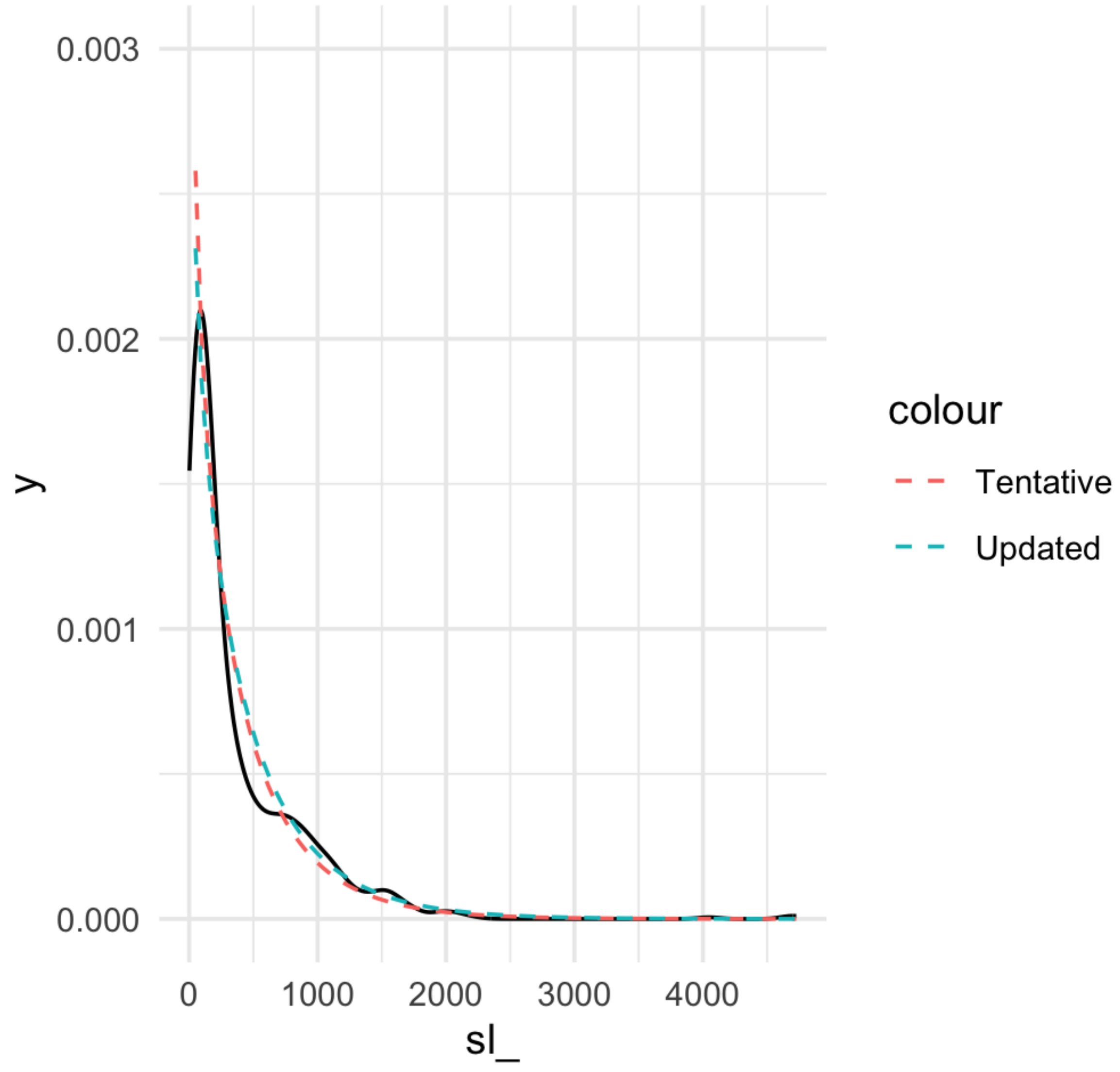
Gamma

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 ($\hat{k}$) and scale ($\hat{q}$) parameters are given by:

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

Updating the tentative distribution

- The function *update_sl_distr()* updates distributions, if there are no interactions (green dashed line).



Interaction with movement:

- We can now start to test, if the step length distribution and thus the displacement depends on covariates.
- We will start by looking, if time of day has an effect.

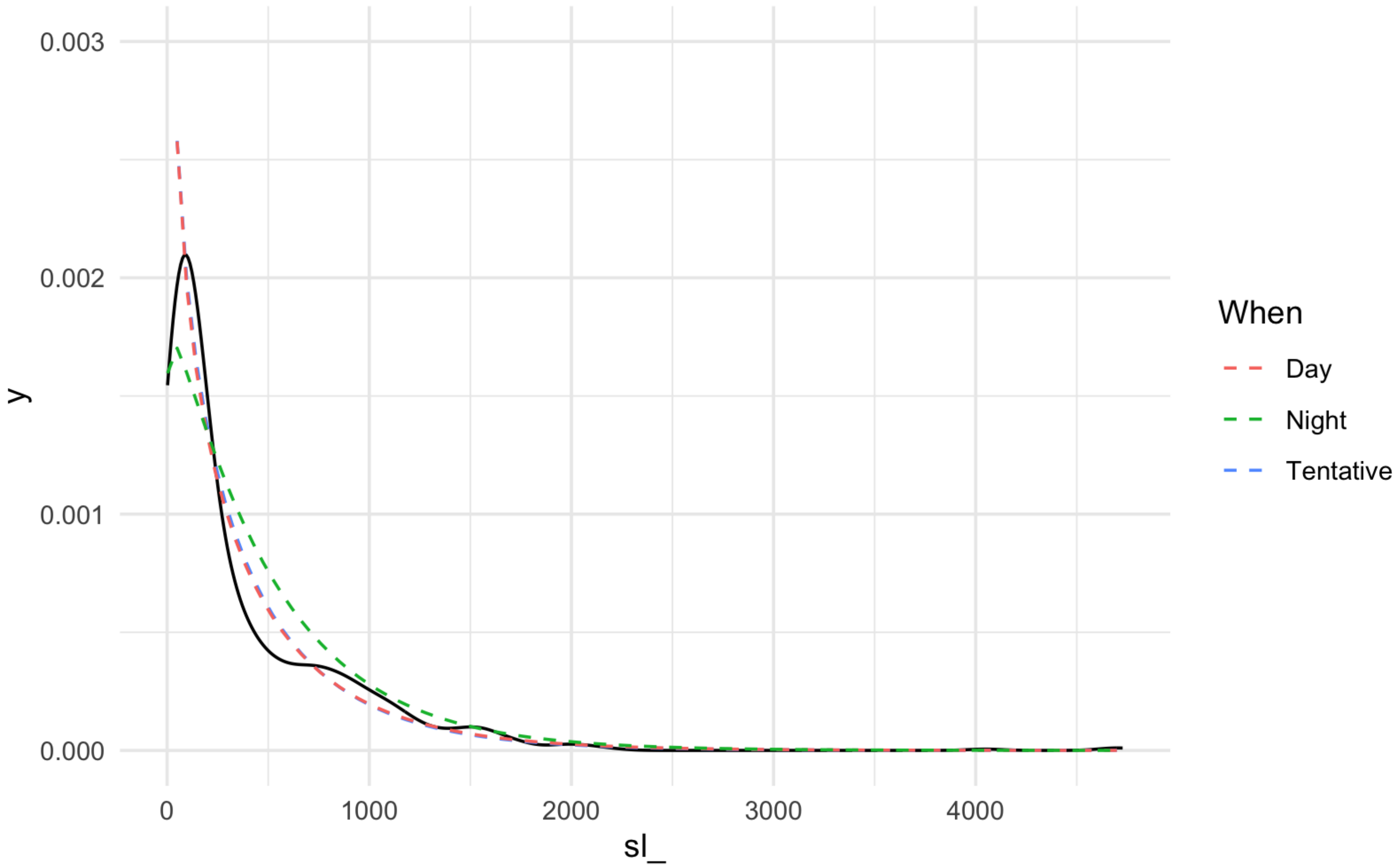
```
m3 <- fit_clogit(
  case_ ~ # This is the response
    dist_forest + # distance to forest
    dist_forest:tod_end_ + # as interaction with time of day

    # Movement kernel
    sl_ +
    log(sl_) +

    # Is movement different for different times?
    sl_:tod_start_ +
    log(sl_):tod_start_ +
    strata(step_id_), # each stratum is an observed step with its r
  data = dat1, # the data
  model = TRUE # to save the input data
)
```

Results of model 3

```
                                coef  exp(coef)   se(coef)       z Pr(>|z|)    
dist_forest                -2.5742862  0.0762082  0.1836126 -14.020  < 2e-16 ***
sl_                         0.0001149  1.0001149  0.0001546   0.743 0.457413    
log(sl_)                   -0.0305555  0.9699066  0.0392698  -0.778 0.436515    
dist_forest:tod_end_night   2.2760978  9.7386039  0.2231104  10.202  < 2e-16 ***
sl_:tod_start_night        -0.0002365  0.9997635  0.0002714  -0.871 0.383546    
log(sl_):tod_start_night    0.3304006  1.3915255  0.0901510   3.665 0.000247 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Updating the step-length distribution

- Updating becomes a bit more tedious.



Lets add some more complexity by adding twilight

- In a final model, I added a third time of day for steps (6 h sampling rate) where the start and the end time of day where different.

```r
dat2 <- dat1 |> mutate(
  tod2 = case_when(
    tod_start_ == "night" & tod_end_ == "night" ~ "night",
    tod_start_ == "day" & tod_end_ == "day" ~ "day",
    .default = "twilight"
  )
)
```

Twilight model

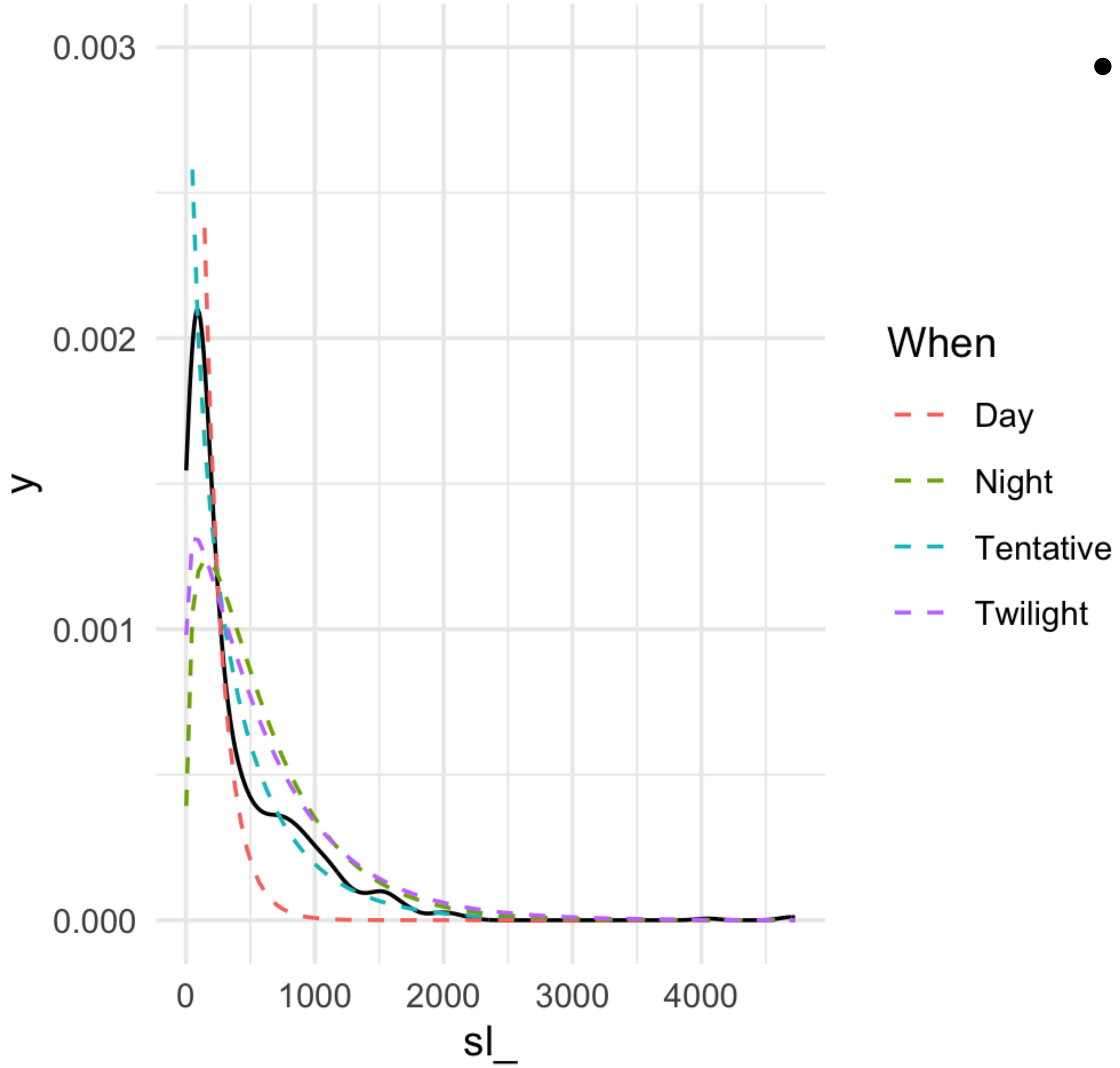
- The model as such is the same, just that tod2 gains one additional level.

```r
m4 <- fit_clogit(
  case_ ~ # This is the response
    dist_forest + # distance to forest
    dist_forest:tod2 + # as interaction with time of day

    # Movement model
    sl_ +
    log(sl_) +

    sl_:tod2 +
    log(sl_):tod2 +
    strata(step_id_),
  data = dat2, # the data
  model = TRUE # to save the input data
)
```

Results of model 4

```
                               coef  exp(coef)   se(coef)      z Pr(>|z|)    
dist_forest              -1.9625610  0.1404981  0.3072839 -6.387 1.69e-10 ***
sl_                      -0.0045351  0.9954752  0.0007024 -6.456 1.07e-10 ***
log(sl_)                  0.1339335  1.1433168  0.0688472  1.945   0.0517 .  
dist_forest:tod2night     0.9187482  2.5061511  0.3989237  2.303   0.0213 *  
dist_forest:tod2twilight  0.5594194  1.7496563  0.3356013  1.667   0.0955 .  
sl_:tod2night             0.0042071  1.0042160  0.0008051  5.225 1.74e-07 ***
sl_:tod2twilight          0.0046655  1.0046764  0.0007210  6.471 9.73e-11 ***
log(sl_):tod2night        0.4670711  1.5953148  0.1843746  2.533   0.0113 *  
log(sl_):tod2twilight     0.2353464  1.2653470  0.0988580  2.381   0.0173 *  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Adjusting the step length distribution



- Clear differences between day and night and twilight.

What about the turn angle distribution?

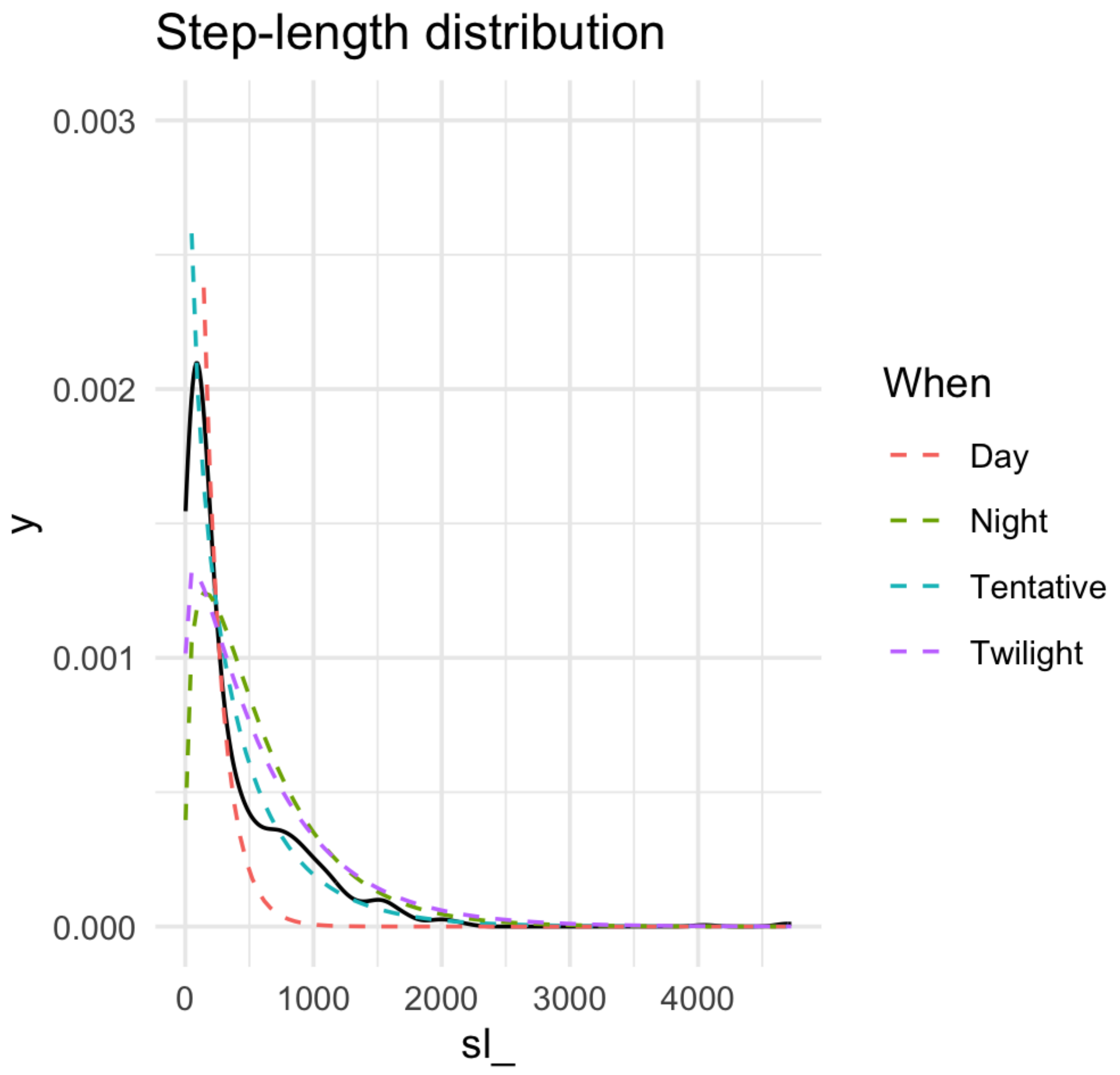
- We can add the turn-angle distribution too to the model.
- Model the concentration parameter (kappa), that is linked to the cosine of turn angle (ta_).

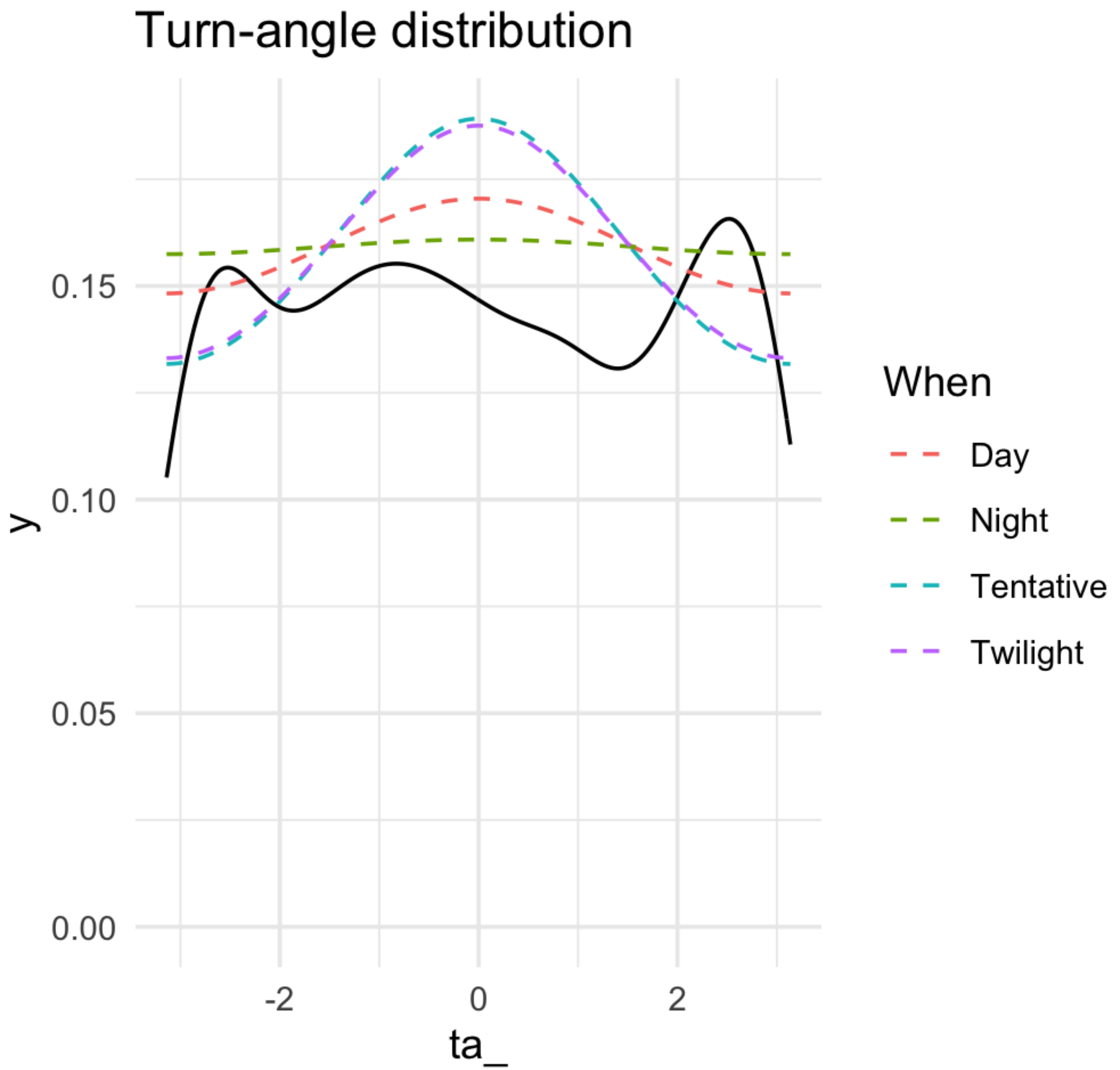
```r
m5 <- fit_clogit(
  case_ ~ # This is the response
    dist_forest + # distance to forest
    dist_forest:tod2 + # as interaction with time of day

    # Movement model
    sl_ +
    log(sl_) +
    cos(ta_) +

    sl_:tod2 +
    log(sl_):tod2 +
    cos(ta_):tod2 +
    strata(step_id_),
  data = dat2, # the data
  model = TRUE # to save the input data
)
```

Results of model 5

```
                                coef  exp(coef)   se(coef)      z Pr(>|z|)    
dist_forest               -1.9347384  0.1444621  0.3077478 -6.287 3.24e-10 ***
sl_                       -0.0045143  0.9954959  0.0006990 -6.459 1.06e-10 ***
log(sl_)                   0.1329933  1.1422423  0.0684373  1.943  0.05198 .  
cos(ta_)                  -0.2506553  0.7782906  0.0890444 -2.815  0.00488 ** 
dist_forest:tod2night      0.9197492  2.5086613  0.3997191  2.301  0.02139 *  
dist_forest:tod2twilight   0.5916826  1.8070263  0.3361230  1.760  0.07835 .  
sl_:tod2night              0.0041849  1.0041936  0.0008014  5.222 1.77e-07 ***
sl_:tod2twilight           0.0046628  1.0046736  0.0007175  6.499 8.09e-11 ***
log(sl_):tod2night         0.4661871  1.5939051  0.1838312  2.536  0.01121 *  
log(sl_):tod2twilight      0.2270334  1.2548718  0.0983935  2.307  0.02103 *  
cos(ta_):tod2night         0.0804597  1.0837852  0.1733877  0.464  0.64262    
cos(ta_):tod2twilight     -0.1016746  0.9033235  0.1169136 -0.870  0.38449    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Movement kernel model 5





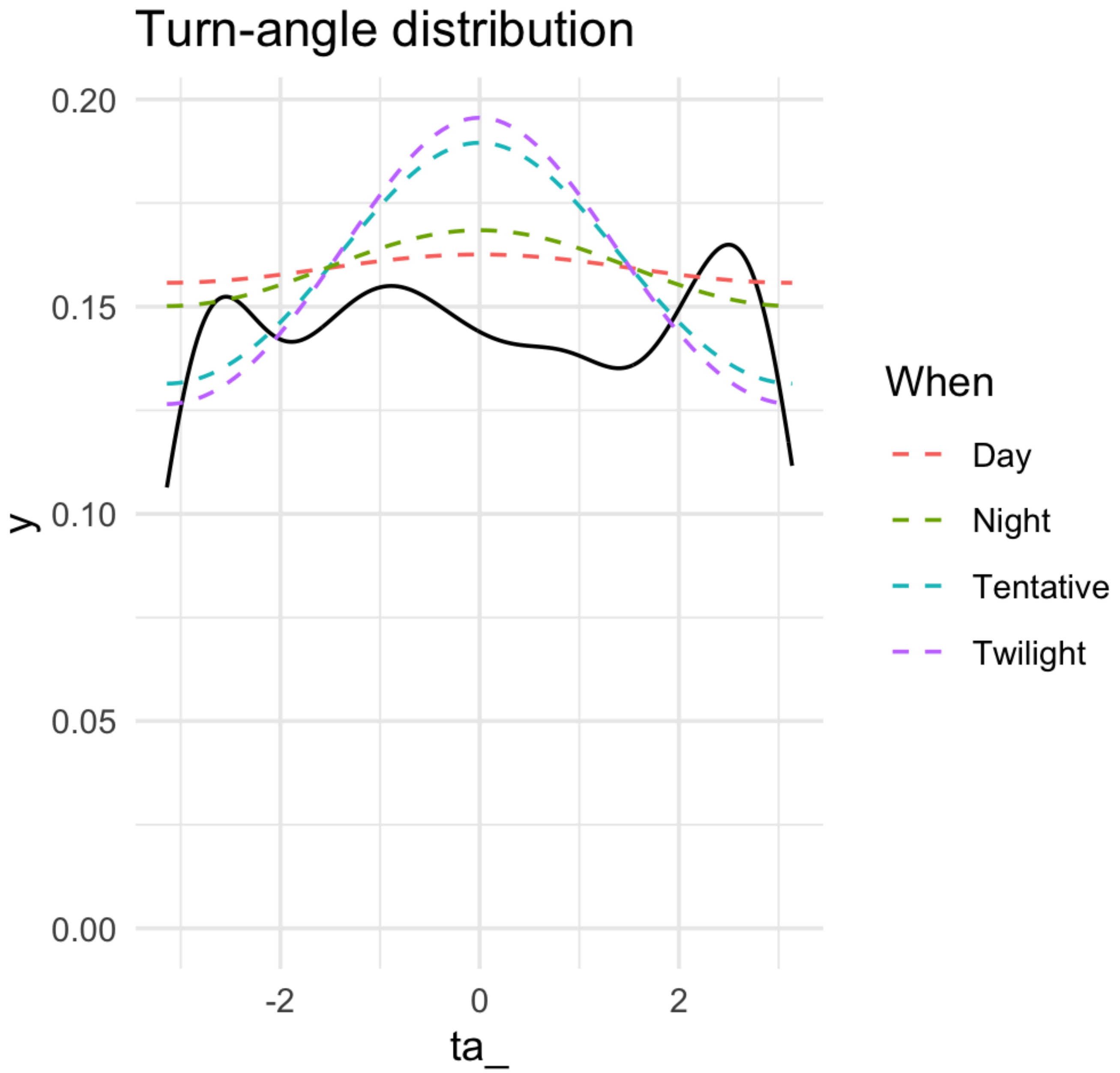
Which model to choose?

- Model 5 seems to be plausible, and is also supported by the AIC.

	df	AIC	dAIC
m0$model	1	3426.735	274.35552
m1$model	2	3322.727	170.34781
m2$model	4	3319.949	167.56913
m3$model	6	3300.236	147.85643
m4$model	9	3177.107	24.72733
m5$model	12	3152.380	0.00000

Conclusion

- Clear difference of habitat selection between different time of days.
- Larger displacement during twilight and night, than during the day.
- Most directed movement during twilight.



Beyond the basics

- Non-linear effects
- Accounting for individual variation
- Account for different behavioral states
- Simulate from a fitted model
- Validate models

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How to account for behavioral states in step-selection

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RESEARCH ARTICLE | Open Access

Using lineups to evaluate goodness of fit of animal movement models

John Fieberg, Smith Freeman, Johannes Signer

Thank you for your attention?

- Happy to take questions now or also later (jsigner@uni-goettingen.de)