

Integrated Step- Selection- Functions (iSSF)

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Animal Movement Course 2025



Some background reading

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APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

Article |  Open Access 

Conceptual and methodological advances in habitat-selection modeling: guidelines for ecology and evolution

Joseph M. Northrup , Eric Vander Wal, Maegwin Bonar, John Fieberg, Michel P. Laforge, Martin Leclerc, Christina M. Prokopenko, Brian D. Gerber

First published: 09 October 2021 | <https://doi.org/10.1002/eap.2470> | Citations: 137

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An introduction to statistical models used to characterize species–habitat associations with animal movement data

Review | [Open access](#) | Published: 17 April 2025

Volume 13, article number 27, (2025) [Cite this article](#)



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Applications of step–selection functions in ecology and conservation

Review | [Open access](#) | Published: 07 February 2014

Volume 2, article number 4, (2014) [Cite this article](#)



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Journal of Animal Ecology

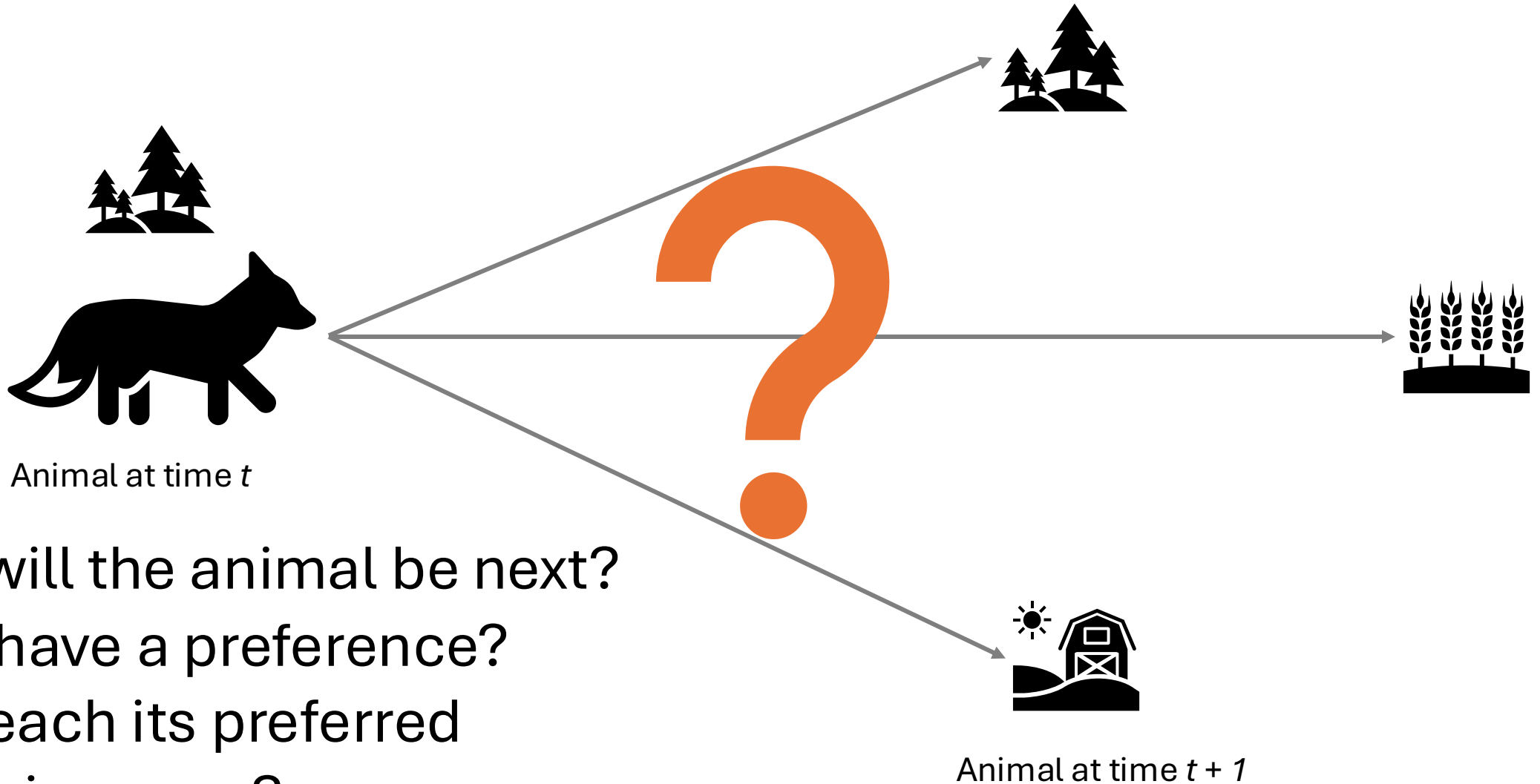
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A ‘How to’ guide for interpreting parameters in habitat-selection analyses

John Fieberg , Johannes Signer, Brian Smith, Tal Avgar

First published: 14 February 2021 | <https://doi.org/10.1111/1365-2656.13441> | Citations: 196

What is it all about?



Where will the animal be next?

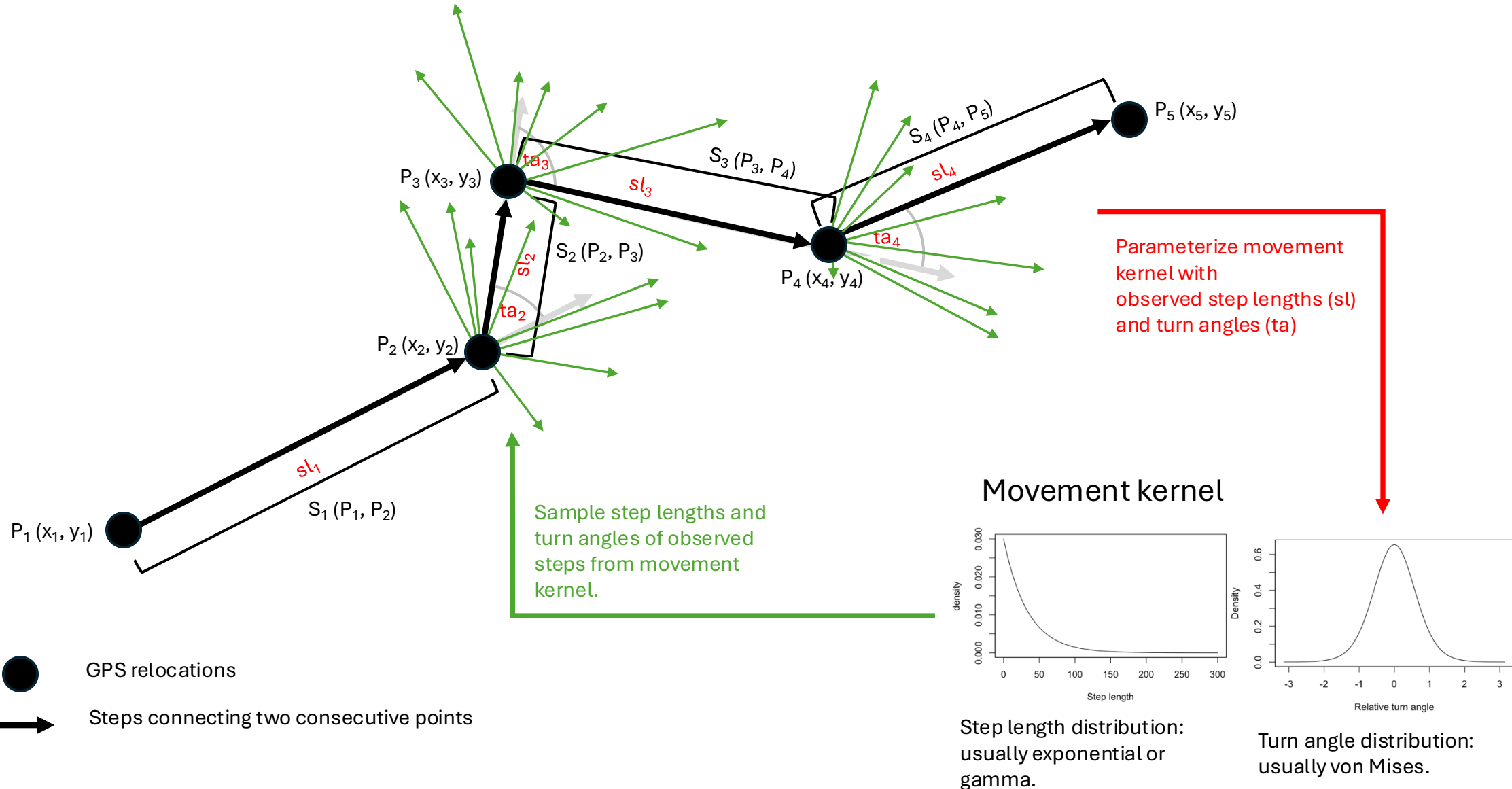
Does it have a preference?

Can it reach its preferred position 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



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.



Standard Paper | [Open Access](#) | CC BY-NC-ND

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**).

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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>	<dtm>		<dtm>		<drtm>		<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)

```
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 likely it is to select a location x_1 relative to a reference location x_2 .

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

```
> 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

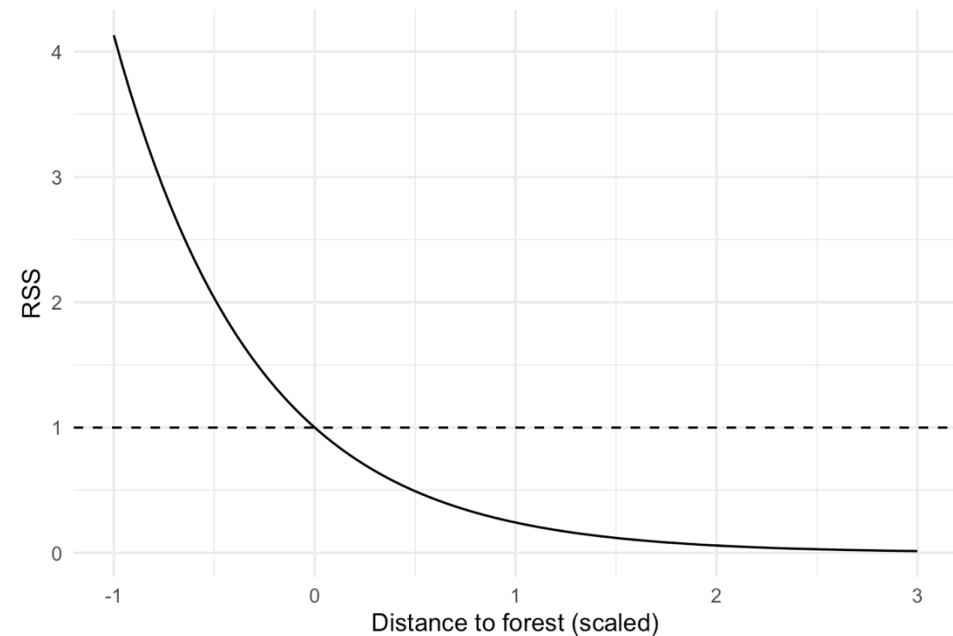
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Relative Selection Strength: Quantifying effect size in habitat- and step-selection inference

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



RSS: Attempt for clarity

- The RSS indicates how much more likely it is to select a location x_1 relative to a reference location x_2 .
- $\text{RSS}(x_2, x_1) = w(x_2) / w(x_1)$

```
> w1 <- exp(coef(m0) * 1)
> w2 <- exp(coef(m0) * 0)
> s1 <- sample(1:2, 1e6, TRUE, prob = c(w1, w2))
> (s2 <- table(s1))
s1
      1      2
199410 800590
> s2[1] / s2[2]
      1
0.2490788
> exp(coef(m0))
dist_forest
      0.2487857
< |
```

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?

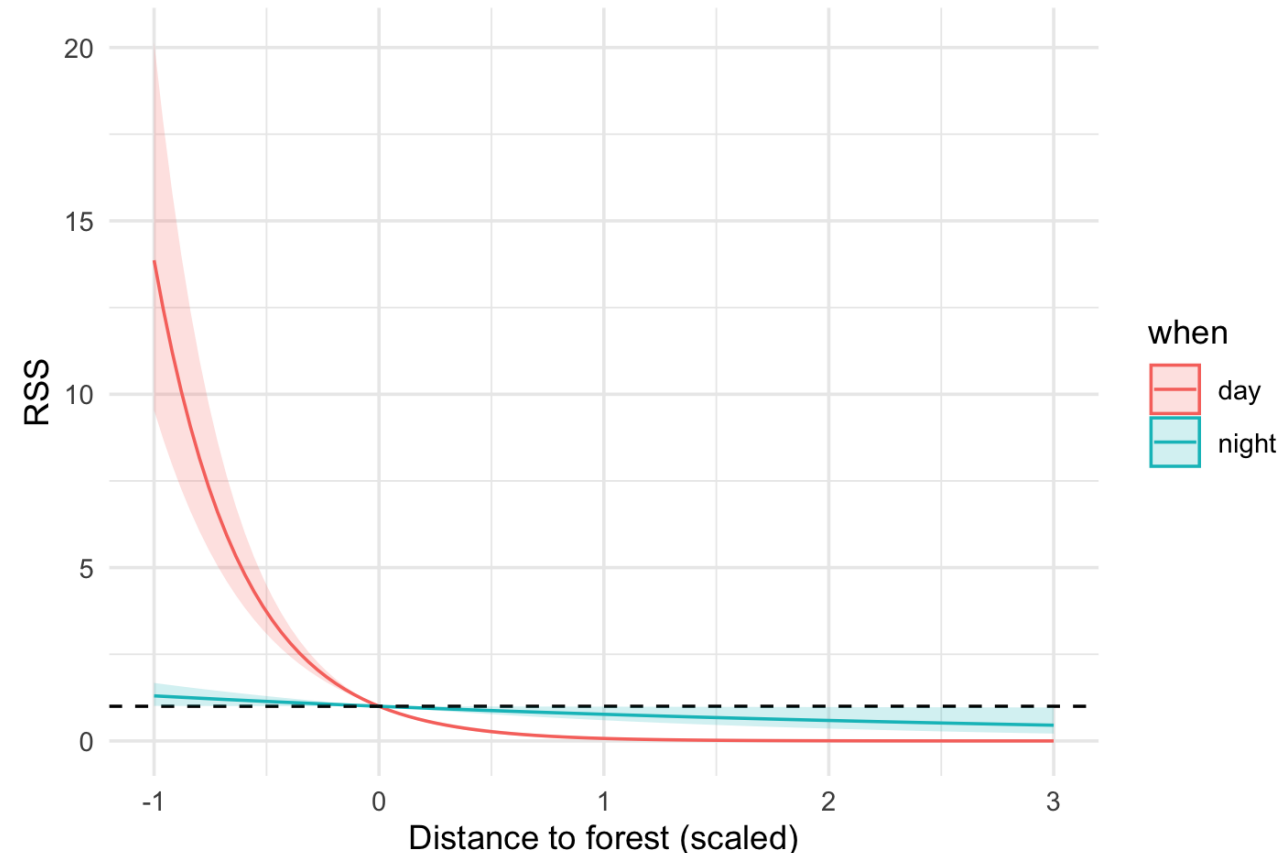
```
m1 <- fit_clogit(  
  case_ ~ # This is the response  
    dist_forest + # distance to forest  
    dist_forest:tod_end_ + # as interaction with time of day  
    strata(step_id_), # each stratum is an observed step with its random  
  steps  
  data = dat1, # the data  
  model = TRUE # to save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

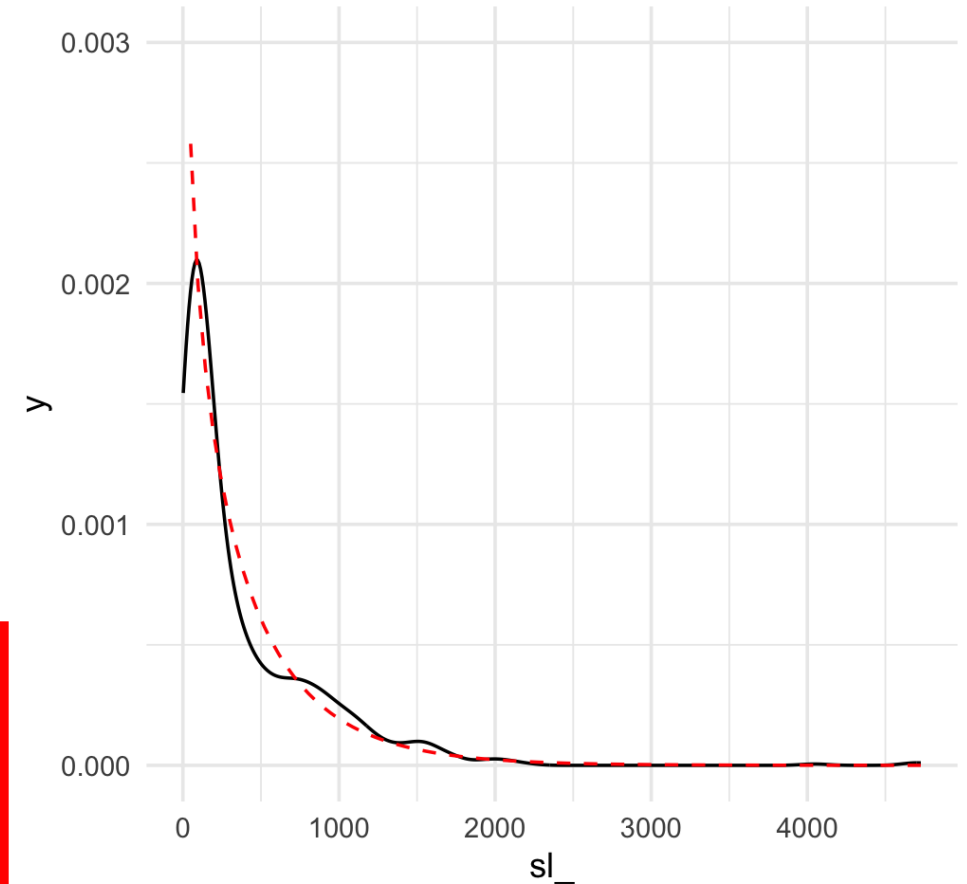
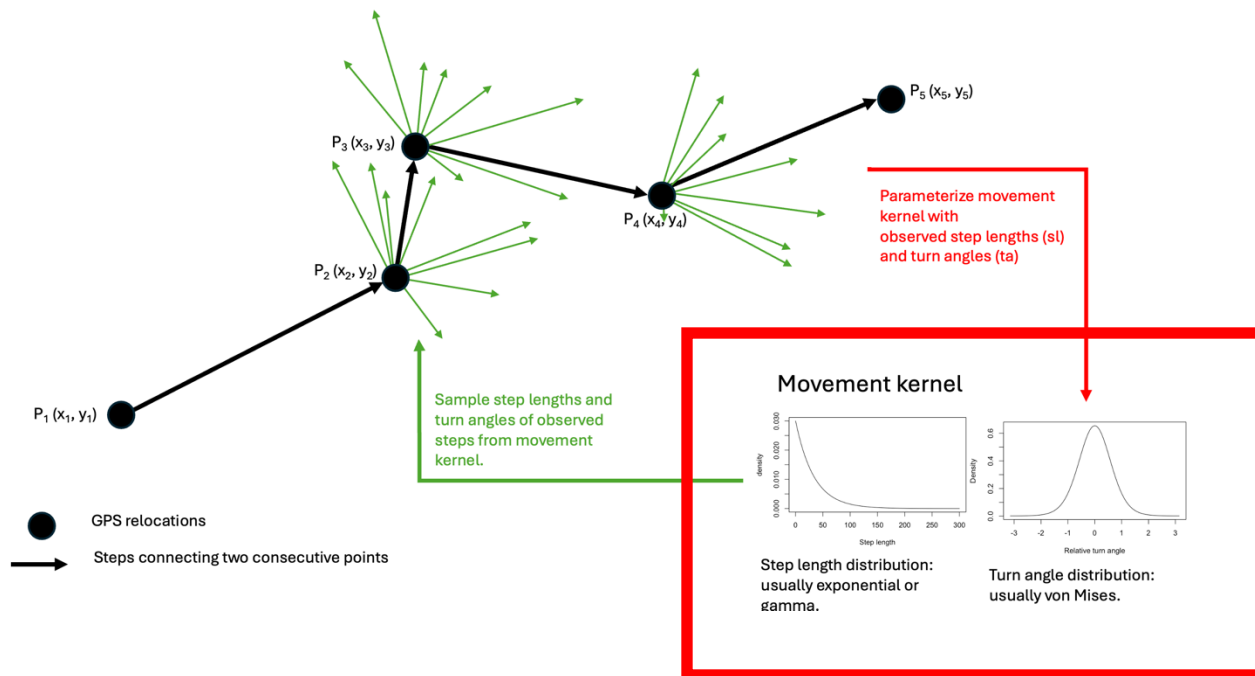
Signif. codes: 0 '***' 0.001 '**' 0.05 '.' 0.1 ' ' 1

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

```
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



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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

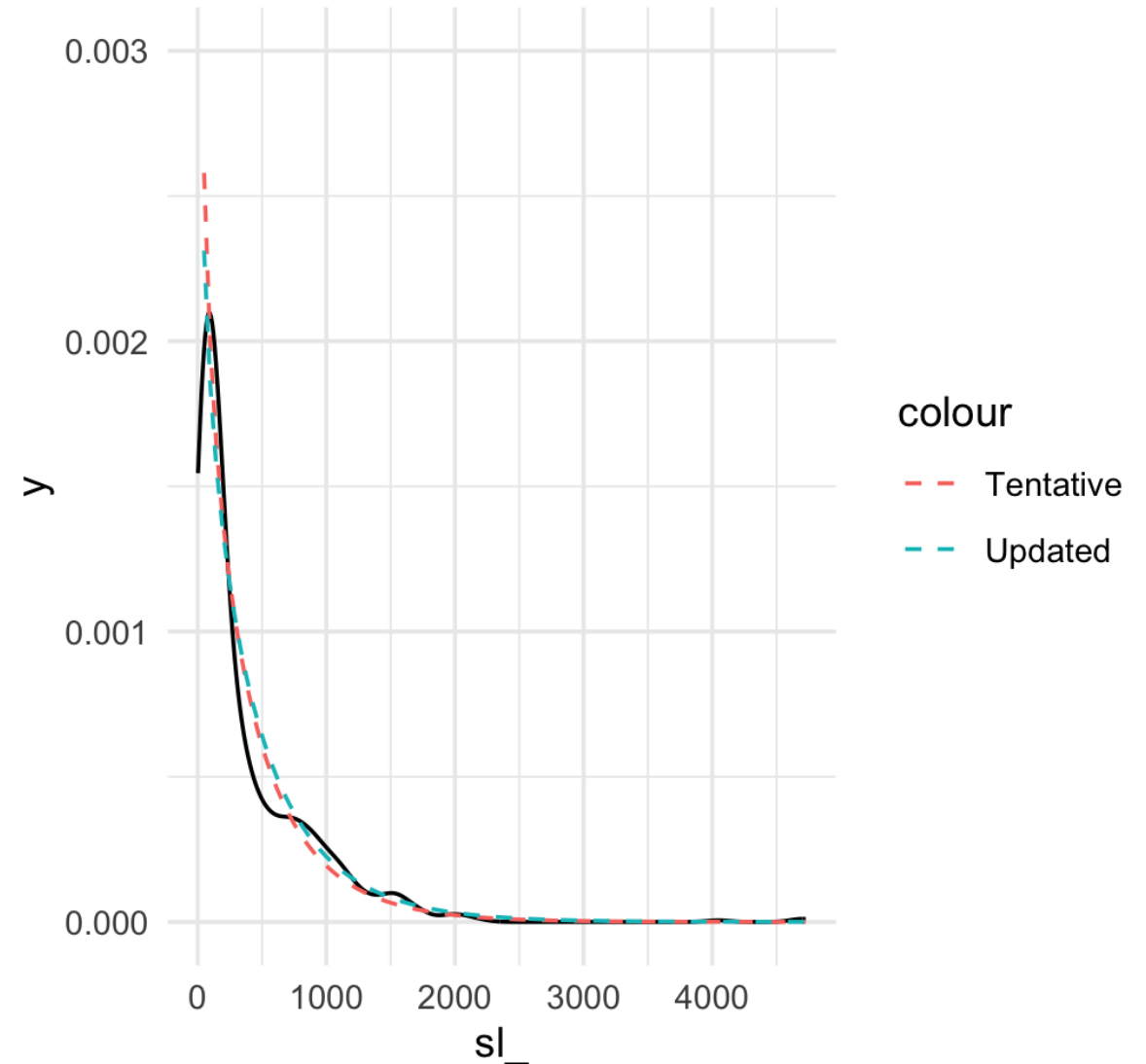
Gamma

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  
)
```

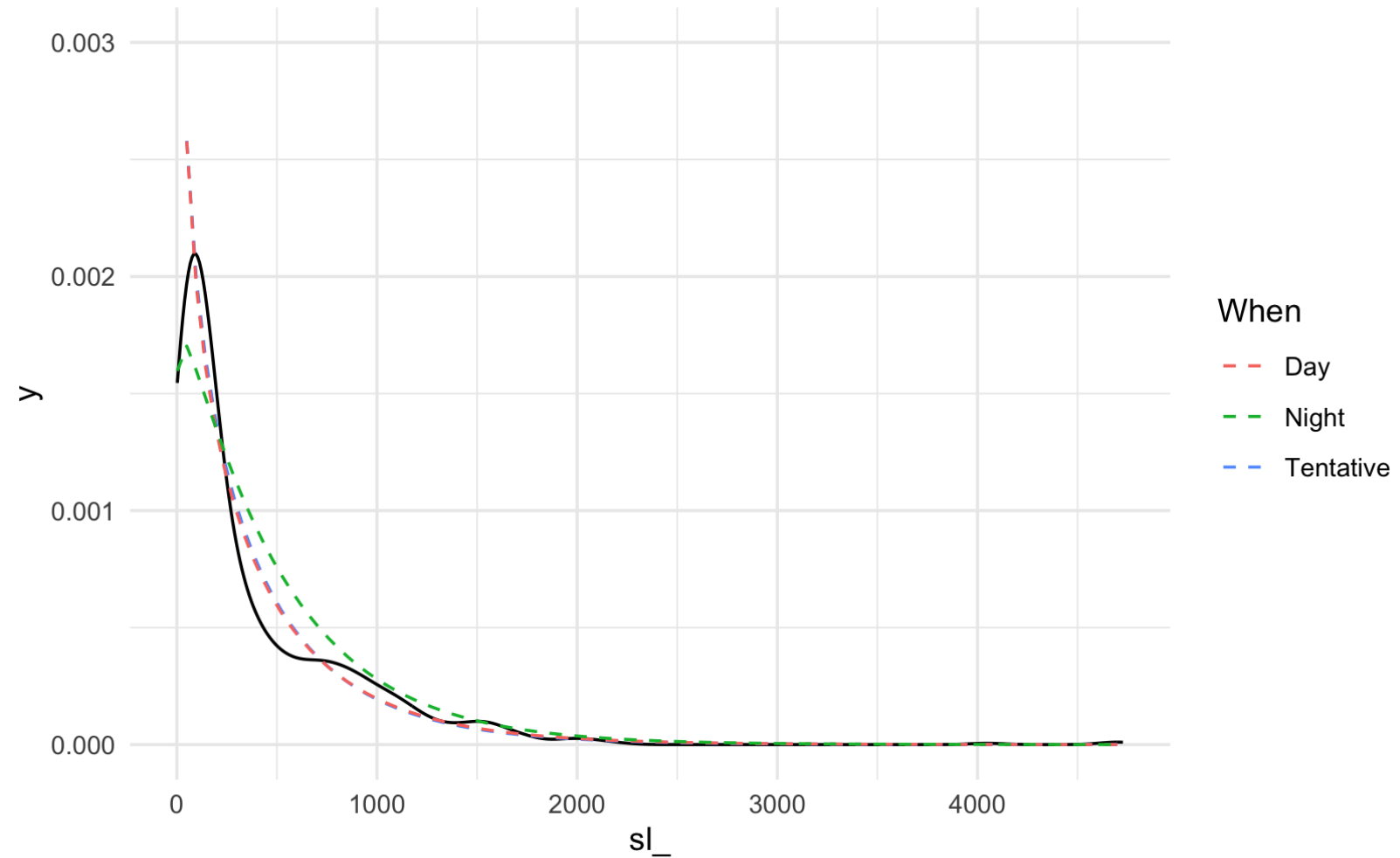
Results of model 3

	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.

```
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.

```
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  
)
```

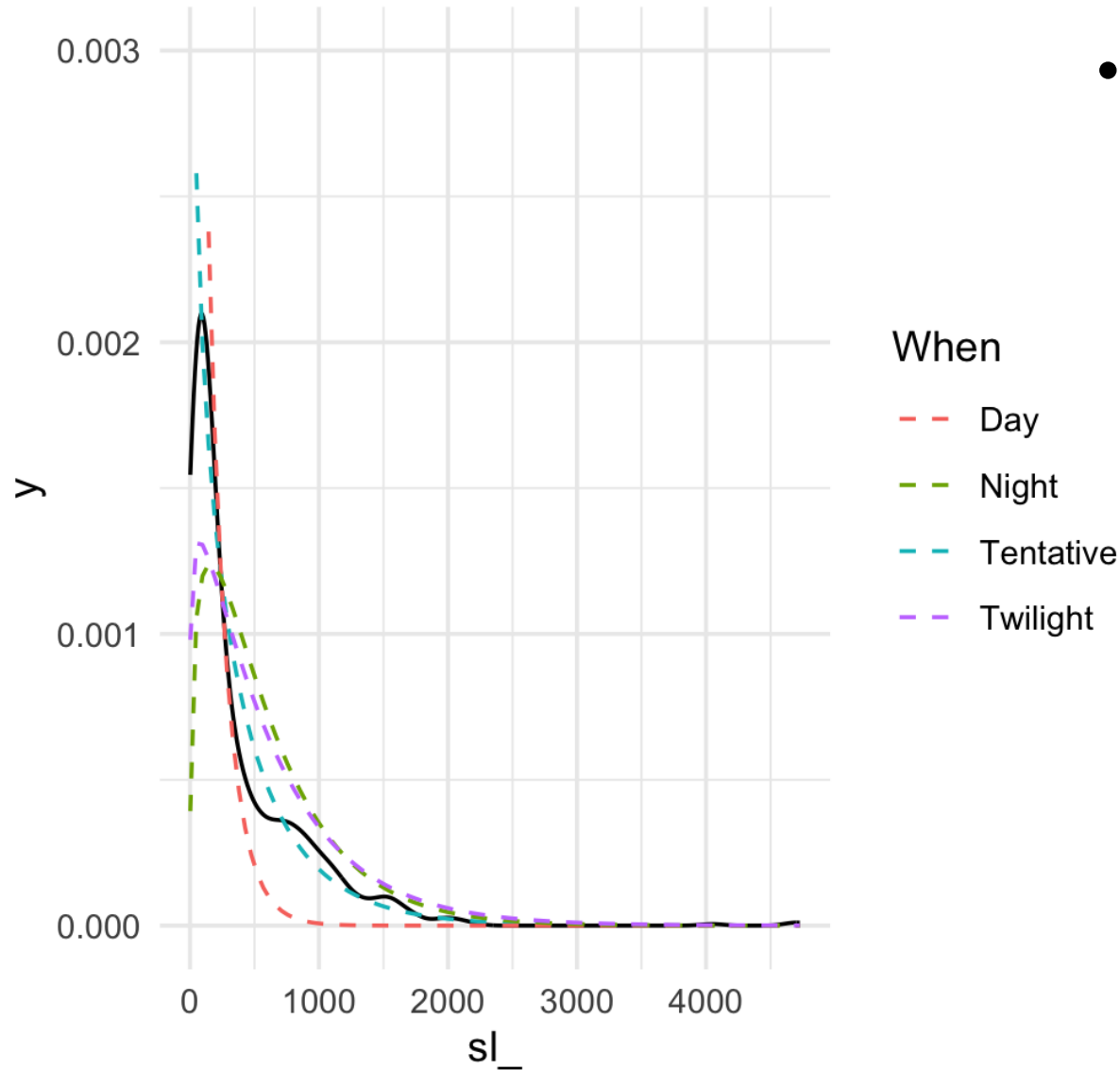

Results of model 4

	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 (κ), that is linked to the cosine of turn angle (ta_{-}).

```
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  
)
```

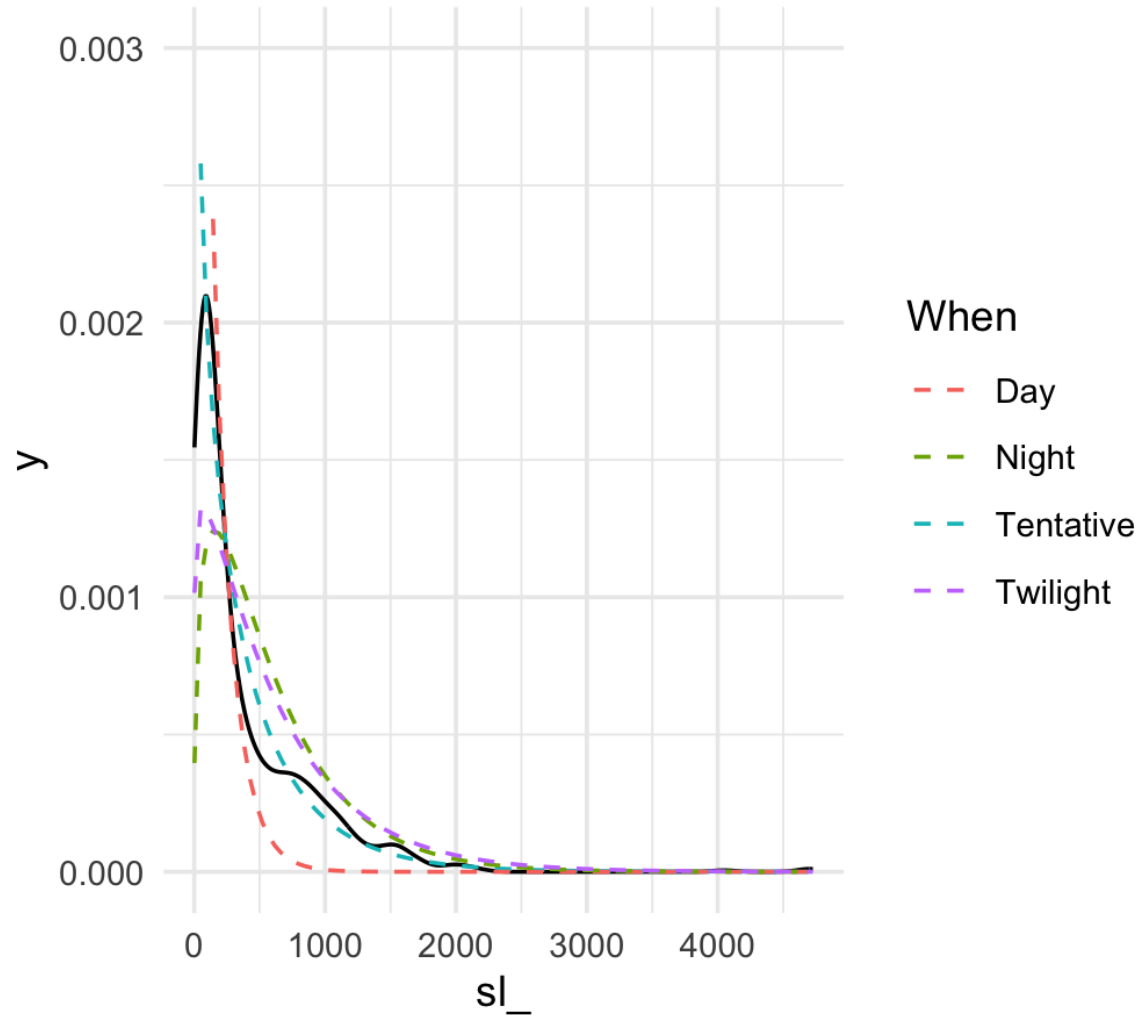
Results of model 5

	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	

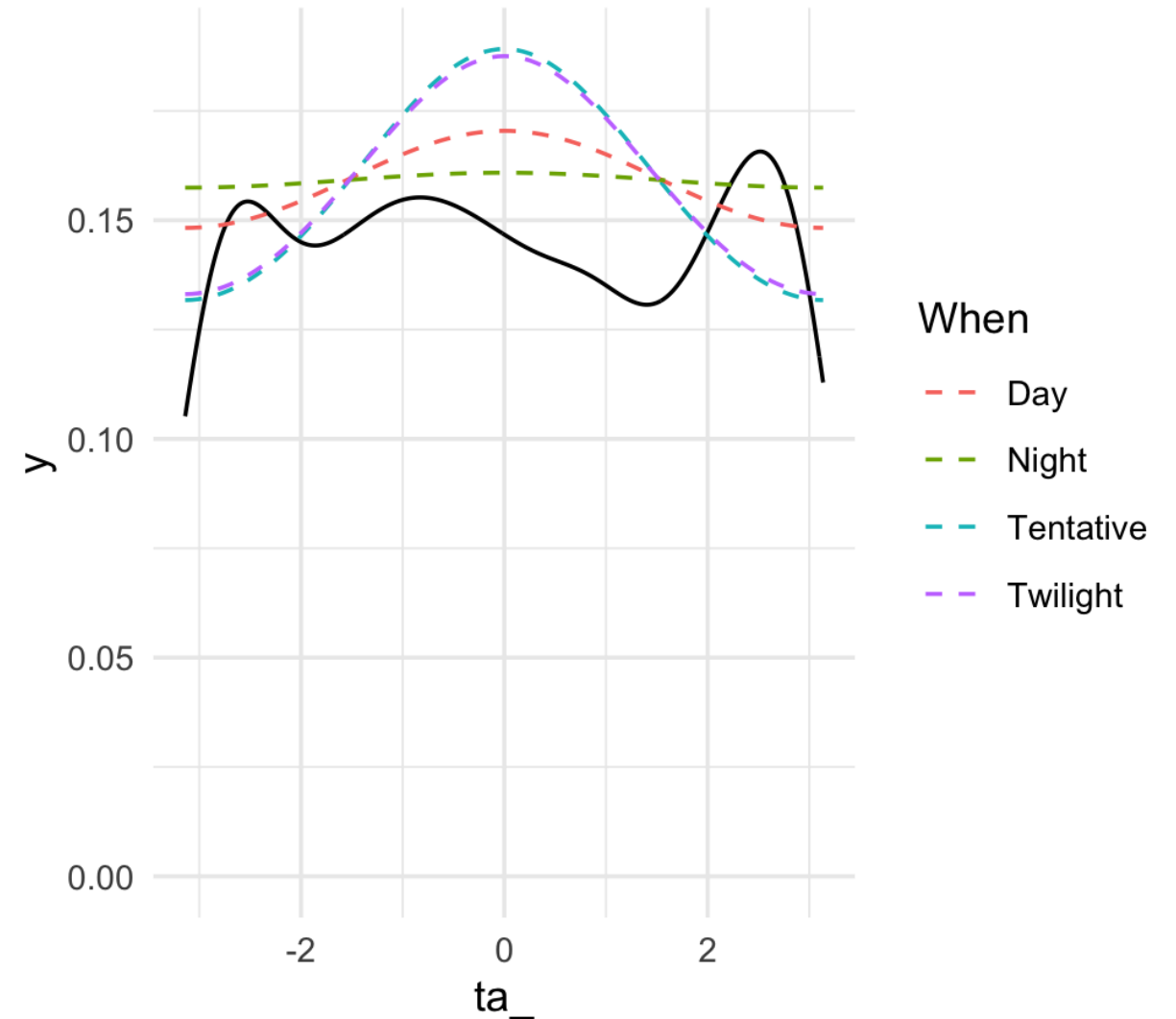
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Movement kernel model 5

Step-length distribution



Turn-angle distribution



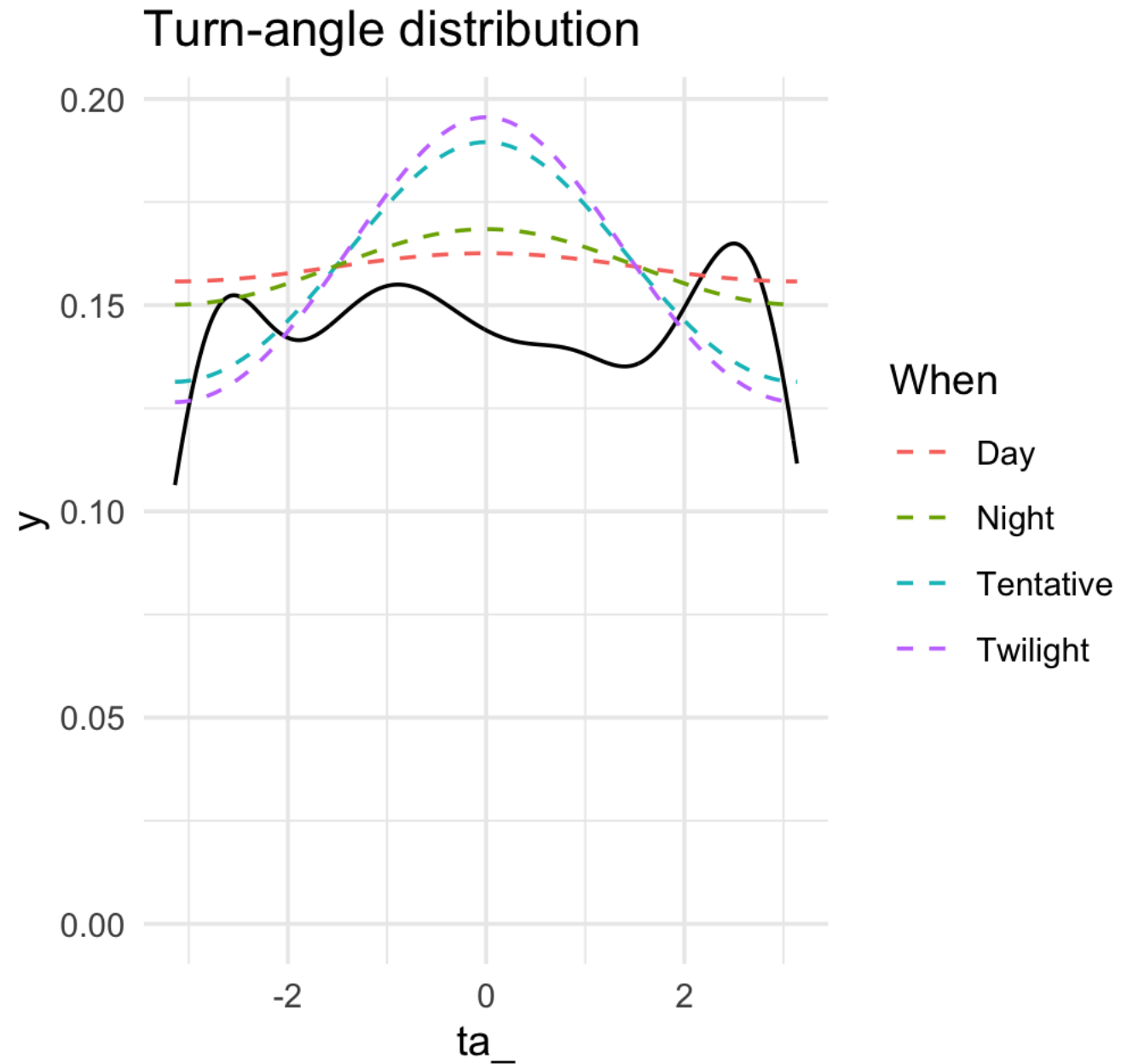
Which model to choose?

- 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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Using lineups to evaluate goodness of fit of animal movement models

John Fieberg Smith Freeman, Johannes Signer