Extensions to ‘classical’ iSSF

Johannes Signer

March 2025

Topics

What to do, if we

- have multiple animals
- have different behavioral modes
- have irregular sampling rates
- want to account for non-linear relationships
- want to account for spatial autocorrelation in covariates
- ...,

Multiple individuals

Why should we care?

- Most telemetry studies have data from many animals.
- Often individual behave very different (and we can fully account for these differences in a model).
- We are often interested in population-level effects (i.e., how would an average animal behave).

How-to account for individual differences

1. *Ignore individuals and fit data to all animals.*
2. Fit an individual model for each individual.
3. Use a mixed-model strategy.

2. Fit an individual model for each individual.

- A somewhat naive approach could be, to fit to each individual animal the model of interests (e.g., a SSF or an iSSF).
- In a next step we can then "do statistics" with the coefficients of the individual model. For example, we could
  - calculate the mean and confidence intervals to obtain population level effects, or
  - use a linear models to relate coefficient values to other explanatory covariates.
- A difficulty is if we have extreme observations or some levels of a categorical covariate is not observed for all animals.

There are different programming strategies, how one could approach such a situation:

a. *Write customized code for each individual.*

b. Use some kind of looping structure (for example a `for`-loop).

c. Use a nest-unnest approach, as we have seen previously (for example with the `purrr` package).

An example of this approach was used in Signer et al. 2019

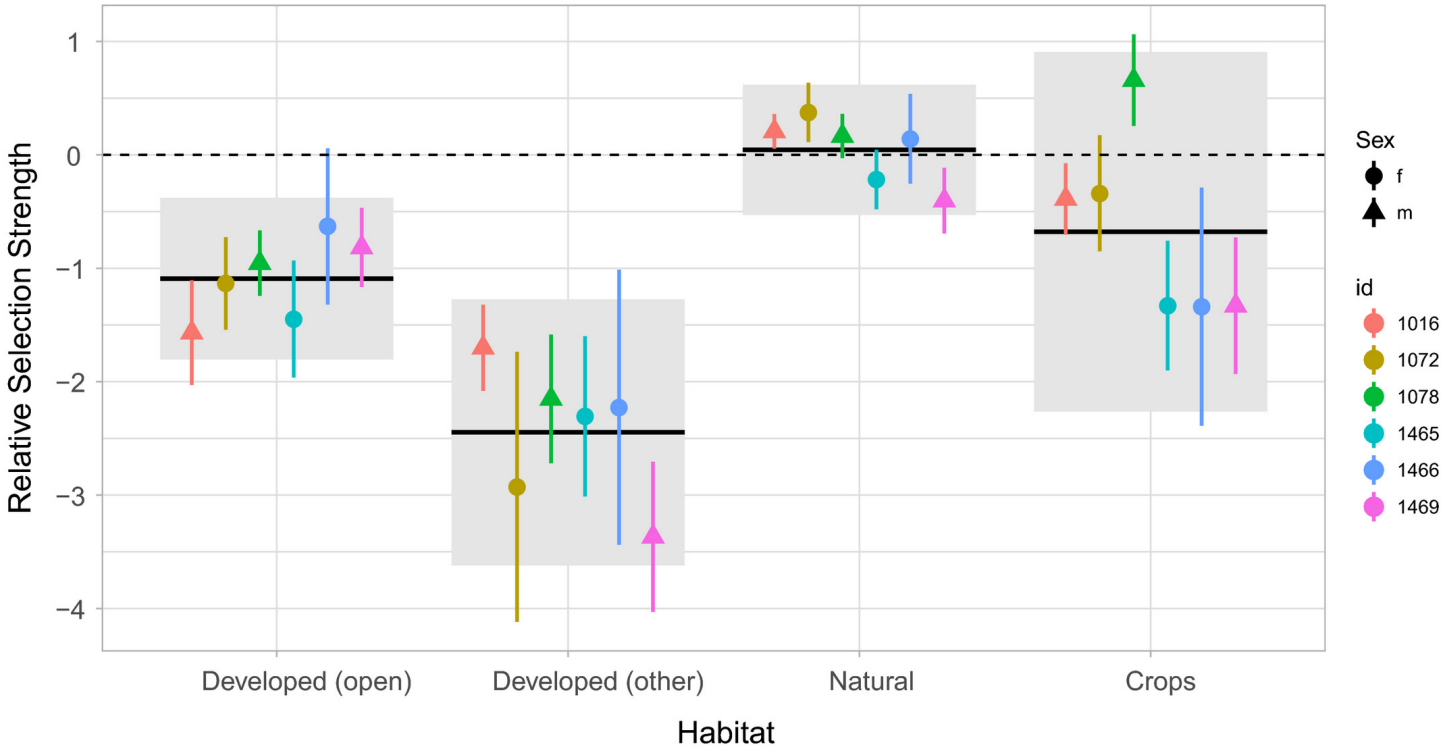

Figure 1: Source Signer et al. 2019

3. Use a mixed-model strategy.

- For HSF this is *relatively* straight forward. We can make use of well established tools that were developed for GLMMs.
- For iSSFs this is slightly more challenging. We have to use a likelihood equivalent reformulation of the iSSF as a poisson regression with random effects for each strata with a fixed large variance.

Random effects for HSFs

- Random effects were proposed for HSFs over 15 years ago[2]

[2] Gillies et al. "Application of random effects to the study of resource selection by animals." Journal of Animal Ecology 75.4 (2006): 887-898.

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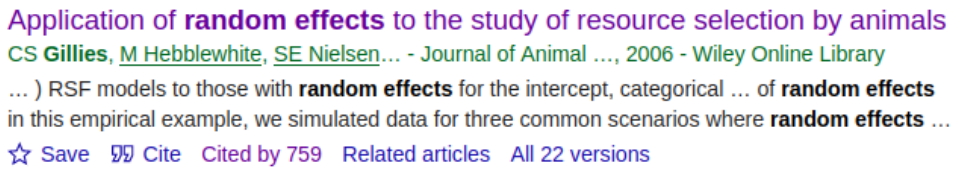
Application of **random effects** to the study of resource selection by animals
CS **Gillies**, M Hebblewhite, SE Nielsen... - Journal of Animal ..., 2006 - Wiley Online Library
...) RSF models to those with **random effects** for the intercept, categorical ... of **random effects**
in this empirical example, we simulated data for three common scenarios where **random effects** ...
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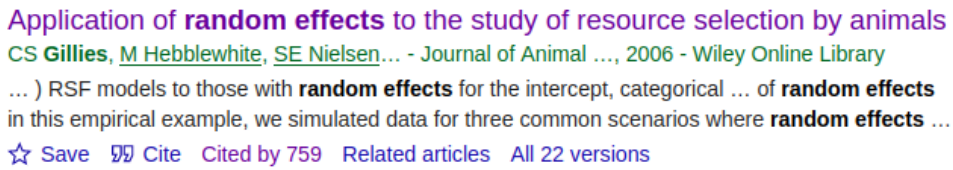
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- Majority of studies between 2016 and 2020 (80 %) only include random intercept and no random slope(s).

[2] Gillies et al. "Application of random effects to the study of resource selection by animals." Journal of Animal Ecology 75.4 (2006): 887-898.

Muff et al. 2020 had another look at this issue and extended this also to iSSF.

BIOLOGGING | Free Access

Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation

Stefanie Muff, Johannes Signer, John Fieberg

First published: 27 August 2019 | https://doi.org/10.1111/1365-2656.13087 | Citations: 88

A case study for HSF/RSF

- Data on habitat selection of Mountain Goats[3]
- Generalized linear model with binomial response (GLM), random intercept (GLMM 1), and random intercept and slopes (GLMM 2).

[3] Lele & Keim, (2006) Weighted distributions and estimation of resource selection probability functions. Ecology 87, 3021–3028.

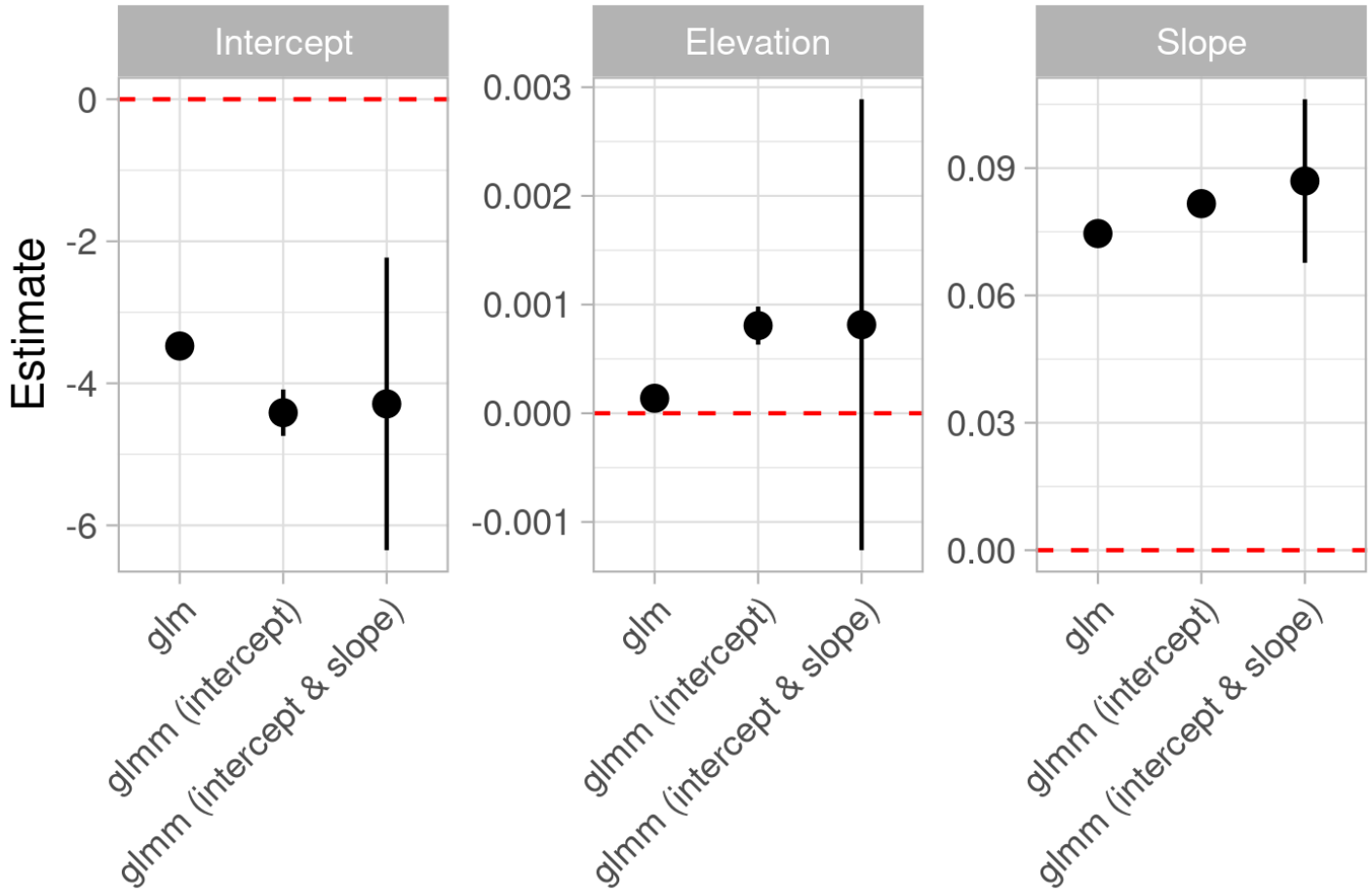
Let us fit three models to tracking data from wild goats:

```
# This is a naive approach (ignoring different animals)
m1 <- glmmTMB(STATUS ~ ELEVATION + SLOPE,
              data = goats, family = binomial())

# This is the random intercept model
m2 <- glmmTMB(STATUS ~ ELEVATION + SLOPE + (1 | ID),
              data = goats, family = binomial())

# This is a random slope and intercept model
m3 <- glmmTMB(STATUS ~ ELEVATION + SLOPE +
                (ELEVATION + SLOPE | ID),
              data = goats, family = binomial())
```

Comparing the model coefficients:



[4] Schielzeth, & Forstmeier. "Conclusions beyond support: overconfident estimates in mixed models." Behavioral Ecology 20.2 (2008): 416-420.

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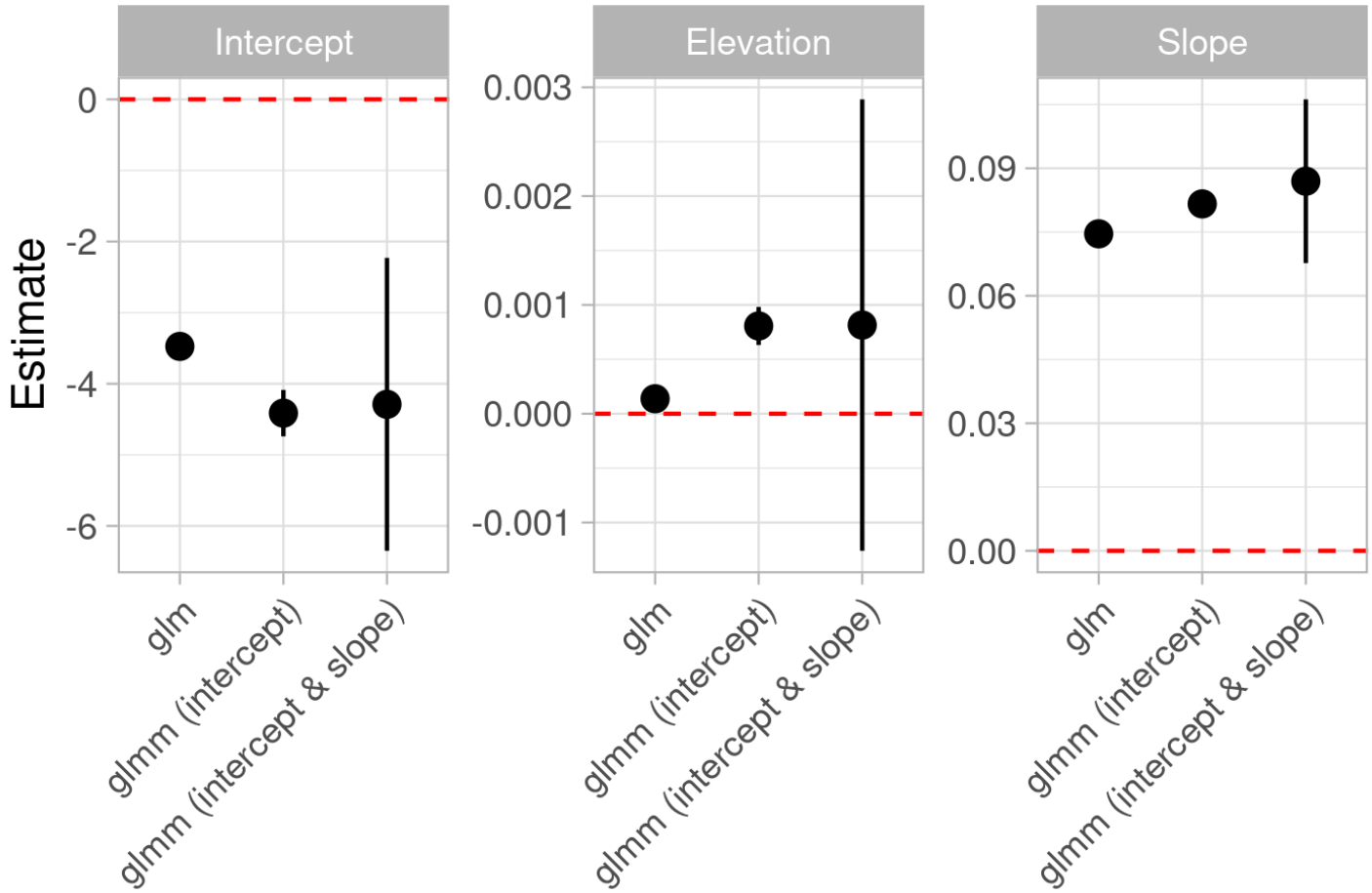


For RSF use random intercept **and** random slope(s)[4].

[4] Schielzeth, & Forstmeier. "Conclusions beyond support: overconfident estimates in mixed models." Behavioral Ecology 20.2 (2008): 416-420.

Accounting for animal-specific variation (SSF)

- Conditional logistic regression with random effects is more difficult.
- The conditional logistic regression is a special case of the multinomial model.
- The multinomial model is likelihood-equivalent to the Poisson model.
- Thus we can rewrite the conditional logistic regression as a Poisson regression.

SSF as poisson model

Reformulation as Poisson model[5] [6]

$$\mathrm{E}(y_{nti}) = \mu_{nti} = \exp(\alpha_{nt} + \boldsymbol{\beta}^\top \boldsymbol{x}_{nti} + \boldsymbol{u}^\top \boldsymbol{z}_{nti}) \ , \quad y_{nti} \sim \mathrm{Po}(\mu_{nti})$$

- $\alpha_{nt} \sim N(0, \sigma_\alpha^2)$ are the stratum specific intercepts with σ_α^2 being fixed at a very large value.
- $\boldsymbol{\beta}^\top \boldsymbol{x}_{nti}$ are the selection coefficients and the design matrix, respectively.
- $\boldsymbol{u}^\top \boldsymbol{z}_{nti}$ specify the random effect structure.

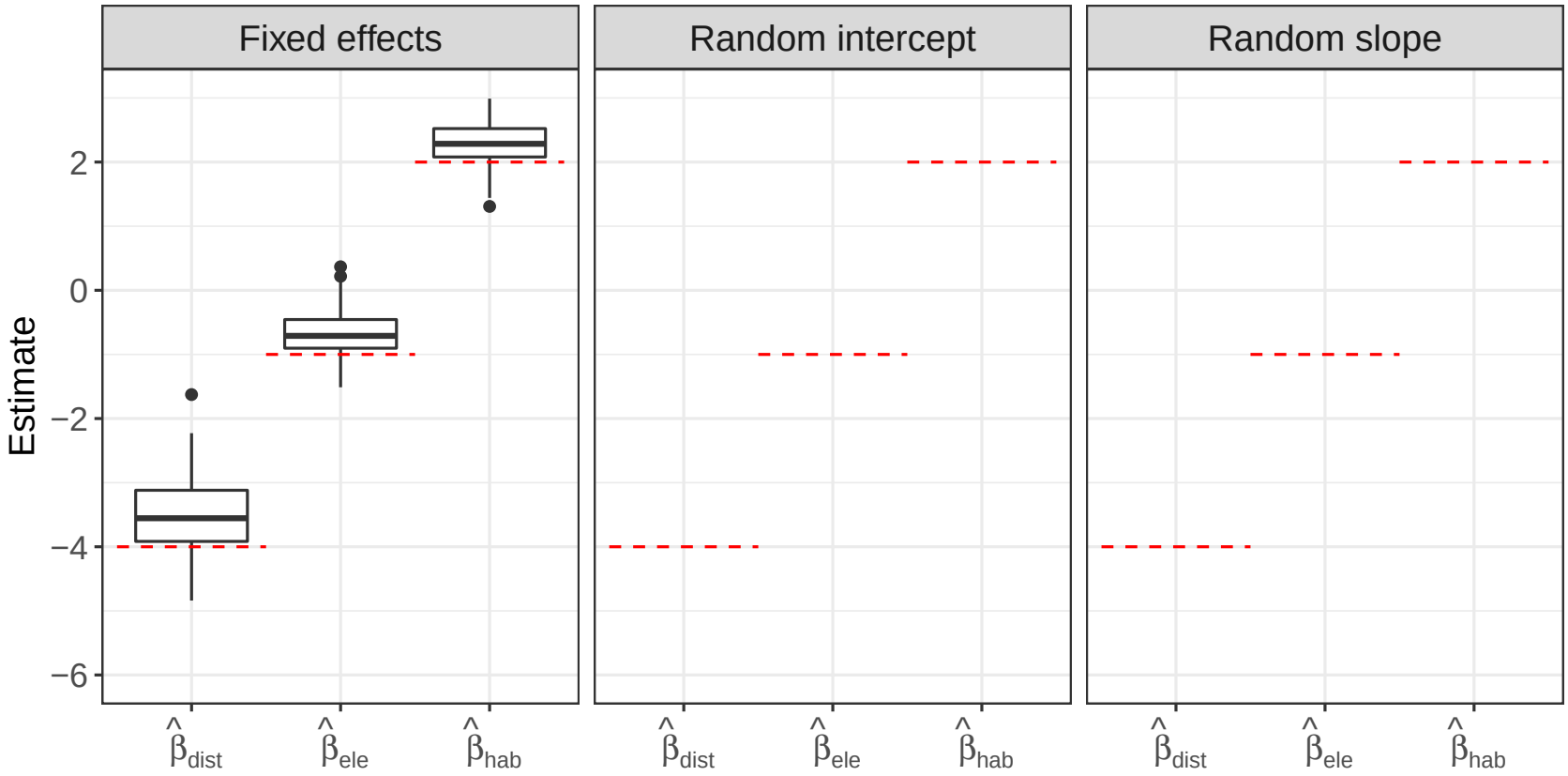
[5] Armstrong et al. "Conditional Poisson models: a flexible alternative to conditional logistic case cross-over analysis." BMC medical research methodology 14.1 (2014): 122.

[6] Muff, S., et al. "Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation". Journal of Animal Ecology, (2020): 89(1), 80-92.

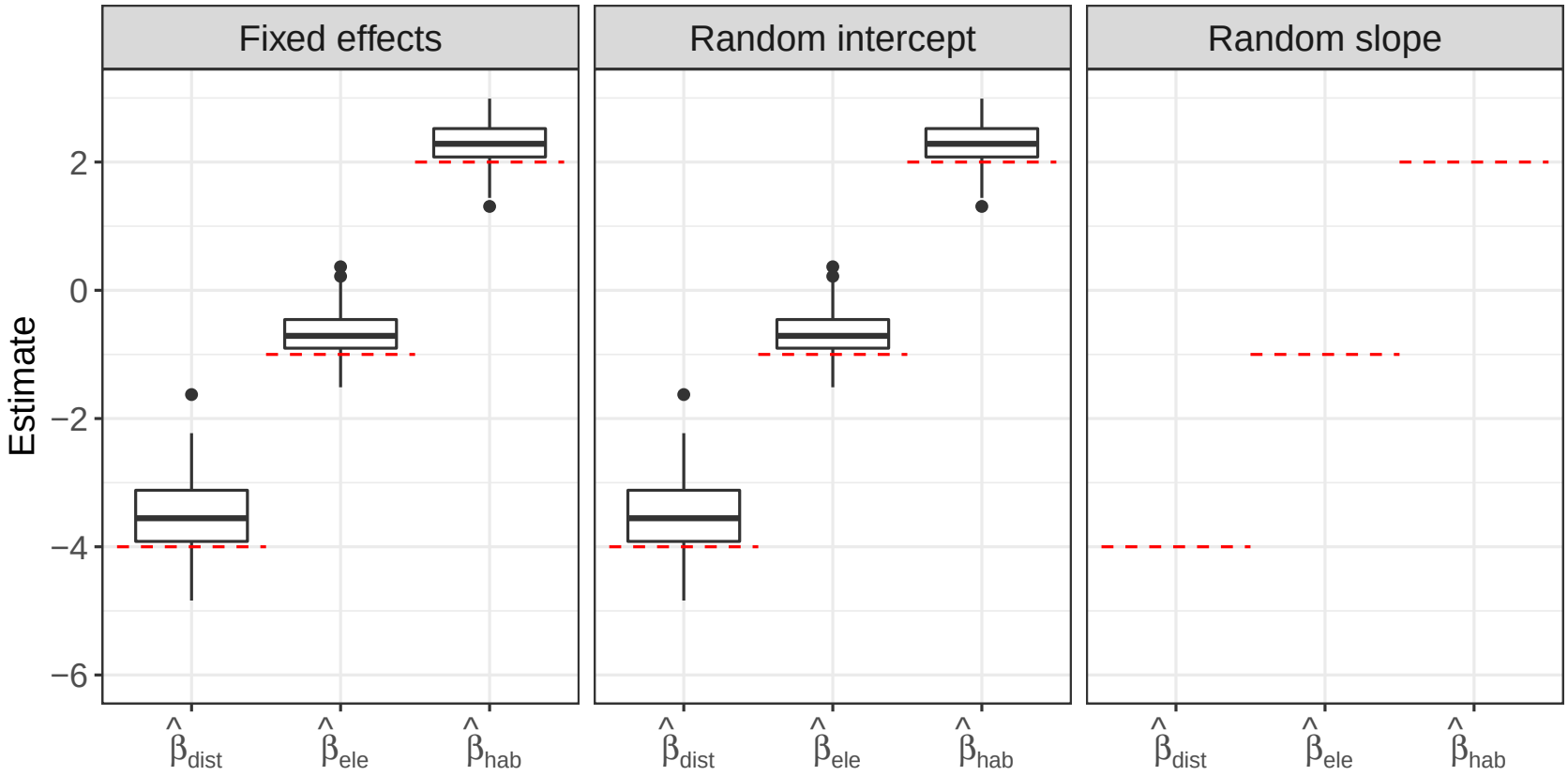
Simulation study from Muff et al. 2020

- Simulation of movement for 20 animals with animal-specific selection coefficients.
- For RSFs sample random points within the availability domain
- For SSFs sample random steps from each location

Results HSF


Fixed effects
Random intercept
Random slope
Estimate
2
0
−2
−4
−6
$\hat{\beta}_{dist}$
$\hat{\beta}_{ele}$
$\hat{\beta}_{hab}$

Results HSF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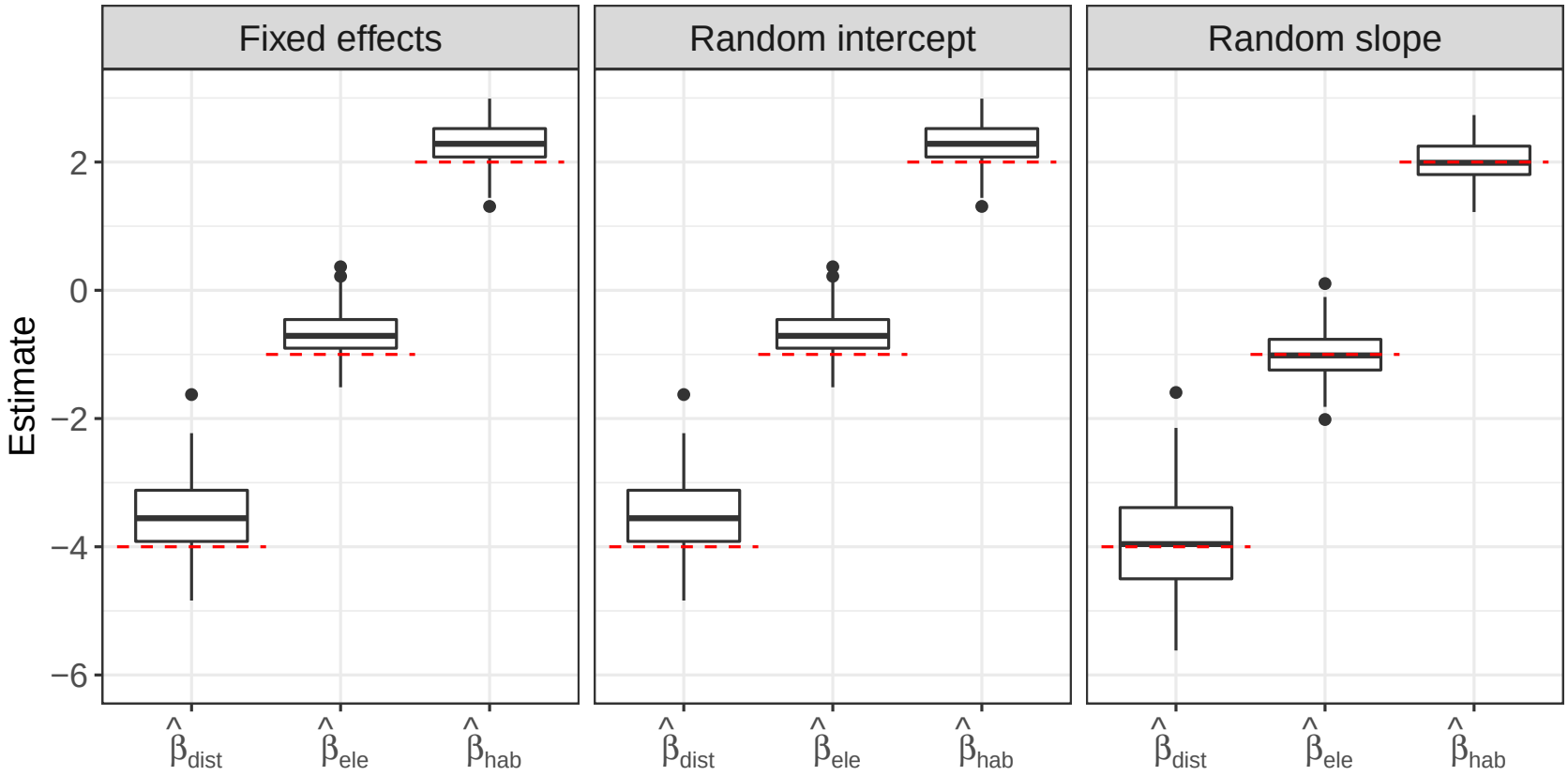
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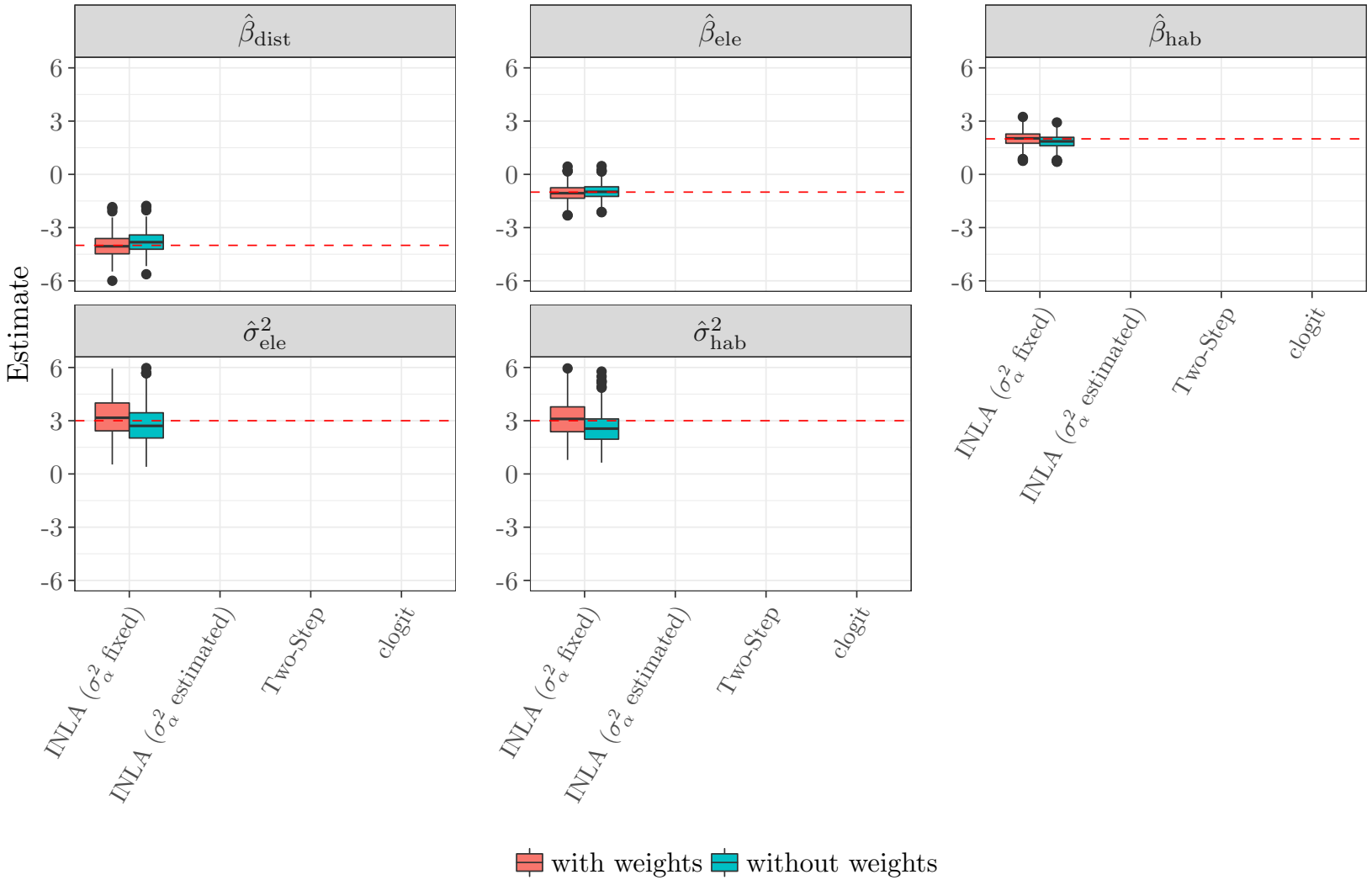
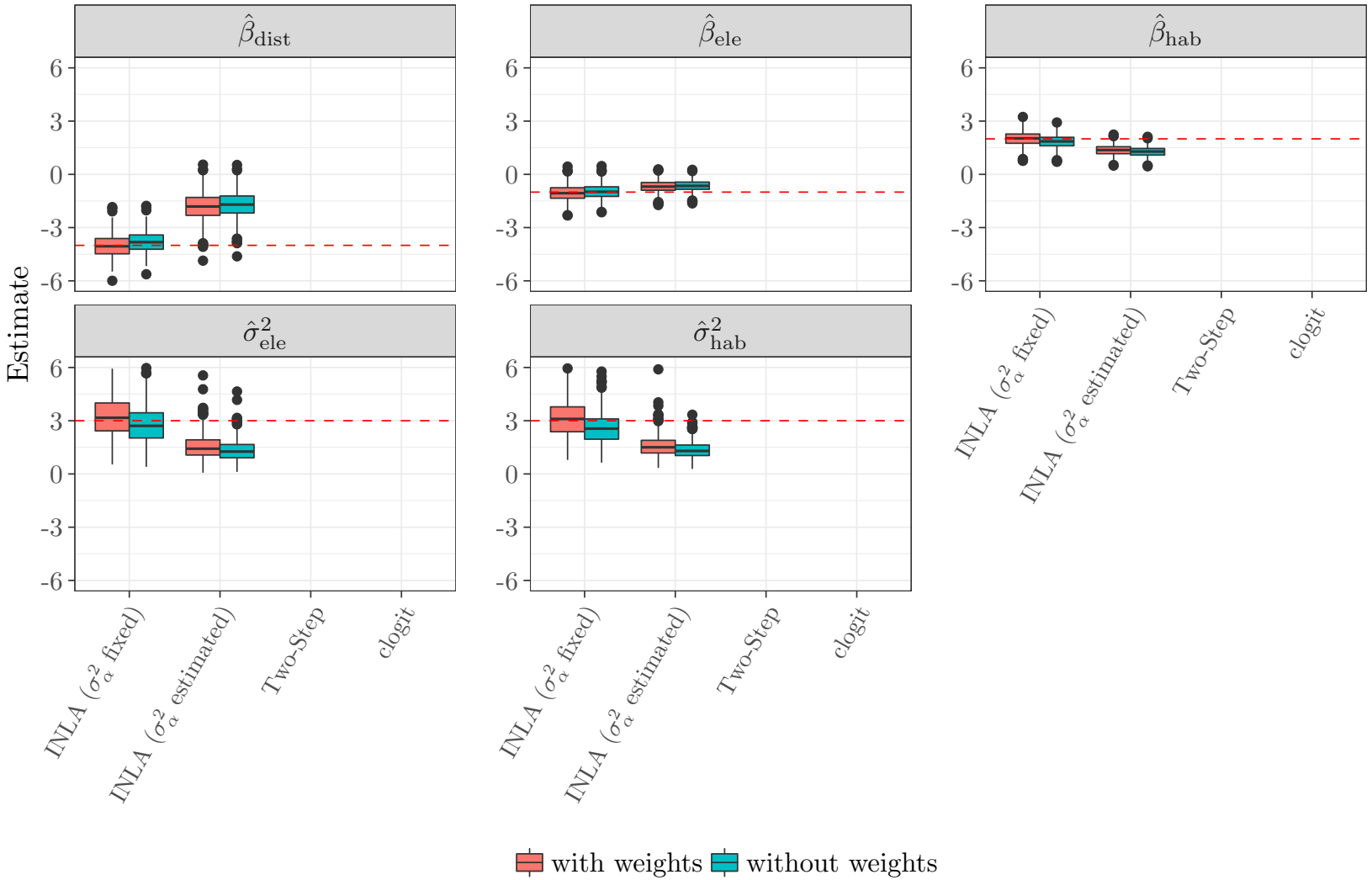
Results SSF


$\hat{\beta}_{\text{dist}}$
$\hat{\beta}_{\text{ele}}$
$\hat{\beta}_{\text{hab}}$
$\hat{\sigma}^2_{\text{ele}}$
$\hat{\sigma}^2_{\text{hab}}$
Estimate
6
3
0
-3
-6
INLA (σ^2_α fixed)
INLA (σ^2_α estimated)
Two-Step
clogit
with weights
without weights

Results SSF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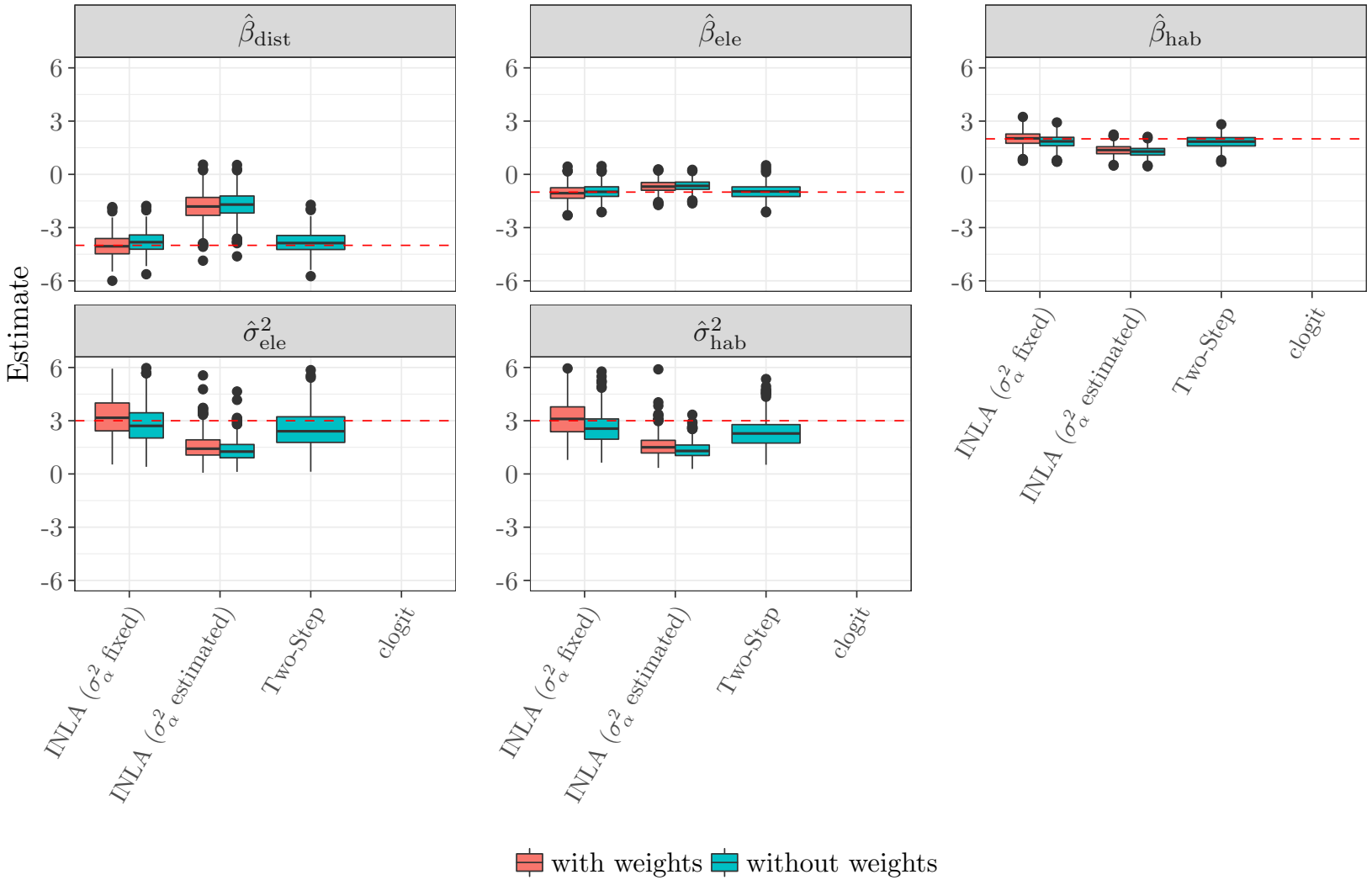
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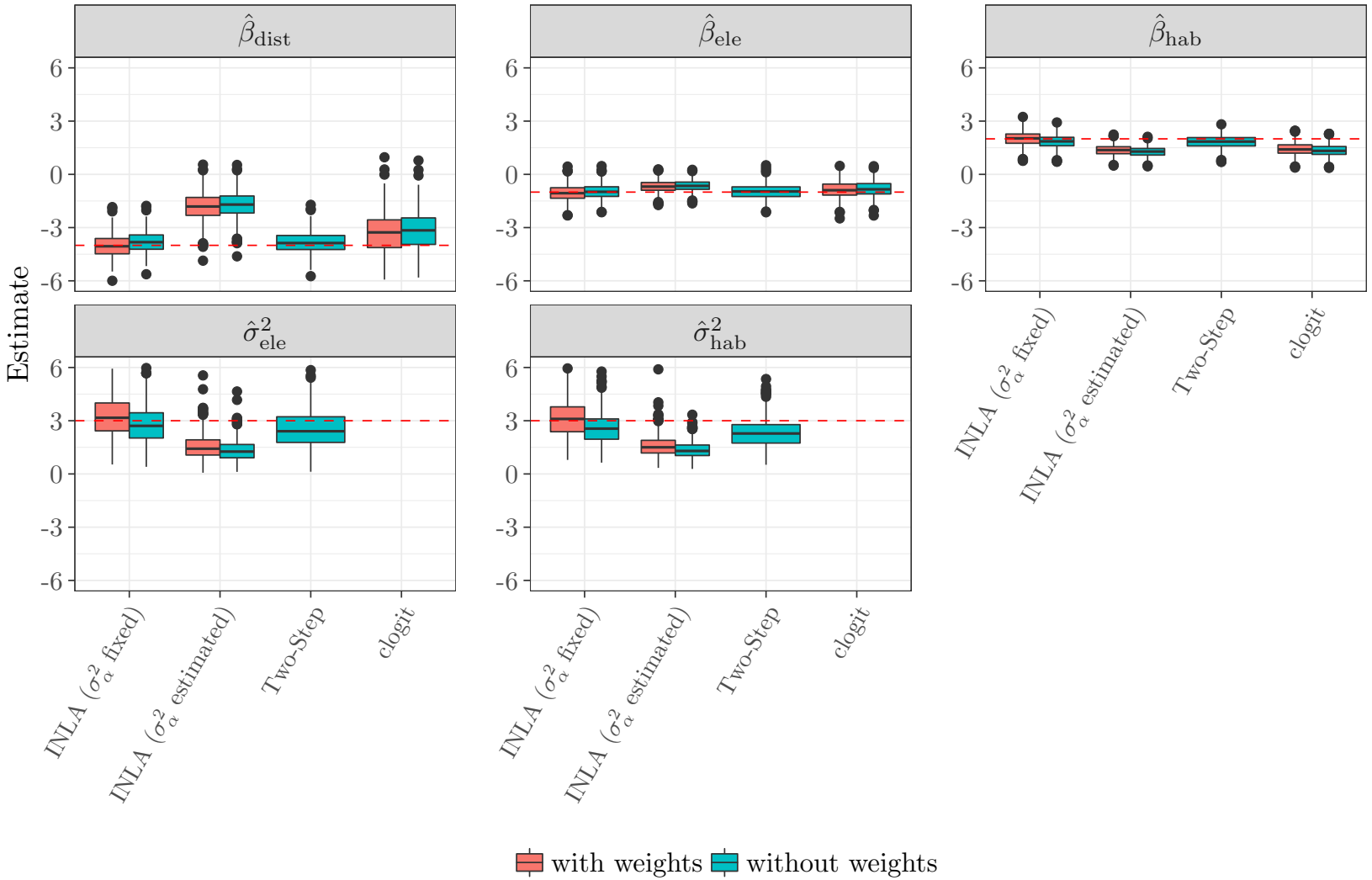
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Software to fit these models

- HSF/RSF:
  - Any standard software package that can fit GLMMs is suitable.
- iSSF:
  - Frequentist: In R the package `glmmTMB` can be use, because it allows to fix the variance of random effects.
  - Muff et al. 2020 primarily used a Bayesian approach (INLA), as it straightforward to fix the variance.

How-to model movement in a mixed-effect context:

RESEARCH ARTICLE | Open Access

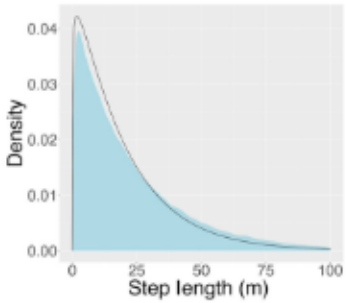
Modelling individual variability in habitat selection and movement using integrated step-selection analysis

Nilanjan Chatterjee, David Wolfson, Dongmin Kim, Juliana Velez, Smith Freeman, Nathan M. Bacheler, Kyle Shertzer, J. Christopher Taylor, John Fieberg

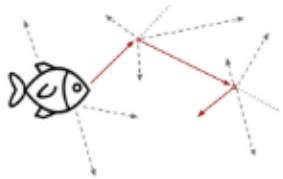
From Chatterjee et al. 2024:

Step one: Prepare data & fit model

1. Fit single sampling kernel for observed step lengths and turn angles using **`amt::fit_distr`**.



2. Generate time-dependent random points and form strata of observed and random steps using **`amt::random_steps`**.



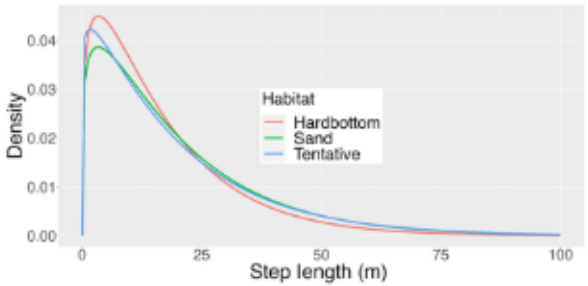
3. Fit mixed-effects conditional logistic regression model using **`glmmTMB::fitTMB`**, assuming step lengths come from a gamma distribution and turn angles from a von Mises distribution,

$$\begin{aligned}\text{case} \sim\ & \text{sl} + \log(\text{sl}) + \cos(\text{ta}) + \\ & \text{x\_start}:(\text{sl} + \log(\text{sl}) + \cos(\text{ta})) + \\ & \text{x\_end} + \\ & (1 \mid \text{step\_id}) + \\ & (0 + \text{sl} + \log(\text{sl}) + \cos(\text{ta}) \mid \text{id}) + \\ & (0 + \text{x\_end} \mid \text{id})\end{aligned}$$

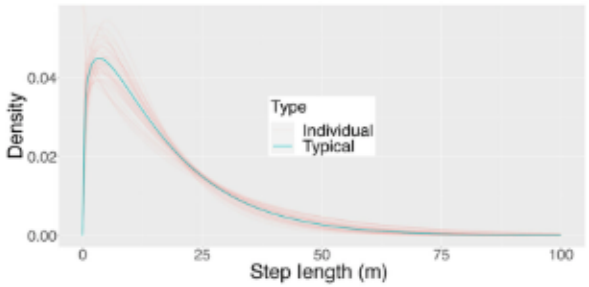
Details are in the caption following the image

Step two: Update movement parameters

4a. **Typical Individual** – Update movement parameters for a typical individual for fixed effects with all random effects set to zero using **`mixedSSA::update_dist`**.

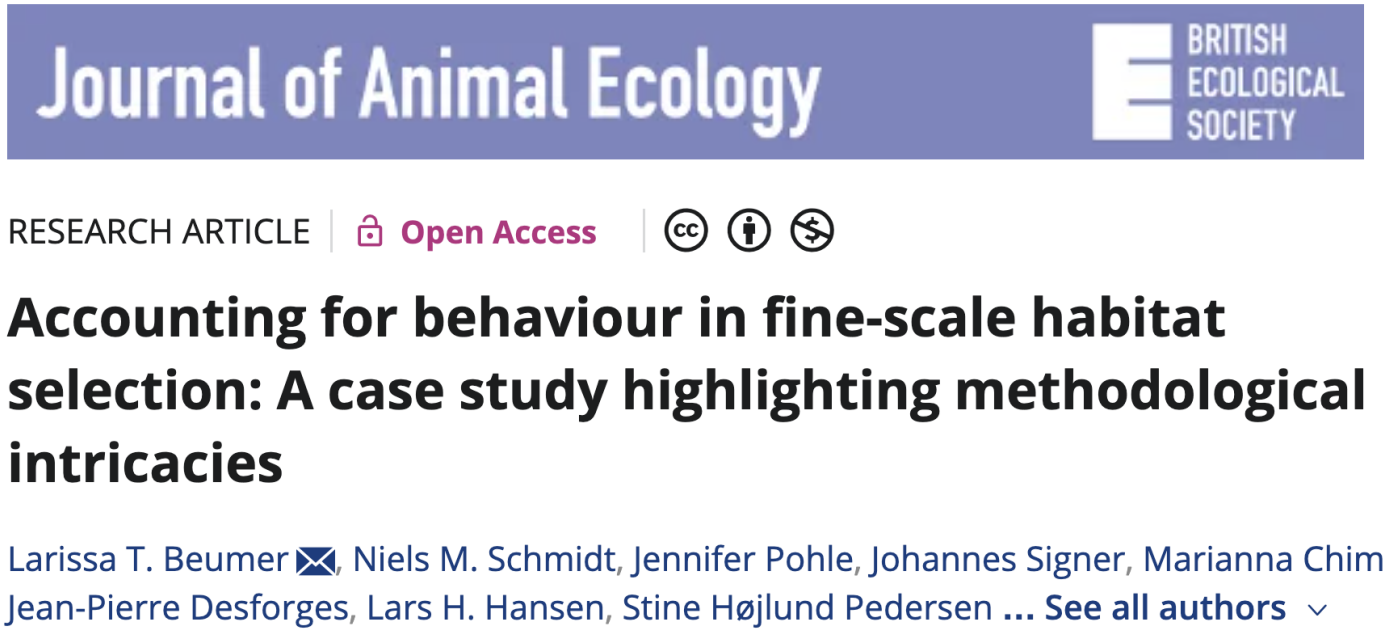


4b. **Individuals** – Update movement parameters for tracked individuals using fixed- and random-effects using **`mixedSSA::update_dist`** with the **`random_effects_var_name`** argument set.



Different behavioral modes

We often want to account for different behavioral modes in habitat selection and movement:



Journal of Animal Ecology

BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE | Open Access

Accounting for behaviour in fine-scale habitat selection: A case study highlighting methodological intricacies

Larissa T. Beumer, Niels M. Schmidt, Jennifer Pohle, Johannes Signer, Marianna Chimienti, Jean-Pierre Desforges, Lars H. Hansen, Stine Højlund Pedersen **... See all authors**

Different behavioral modes

We often want to account for different behavioral modes in habitat selection and movement:

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Article | Full Access

Behavior-specific habitat selection by African lions may promote their persistence in a human-dominated landscape

Justin P. Suraci, Laurence G. Frank, Alayne Oriol-Cotterill, Steve Ekwanga, Terrie M. Williams, Christopher C. Wilmers

First published: 03 February 2019 | https://doi.org/10.1002/ecy.2644 | Citations: 64

Different behavioral modes

We often want to account for different behavioral modes in habitat selection and movement:

Journal of Applied Ecology
BRITISH ECOLOGICAL SOCIETY

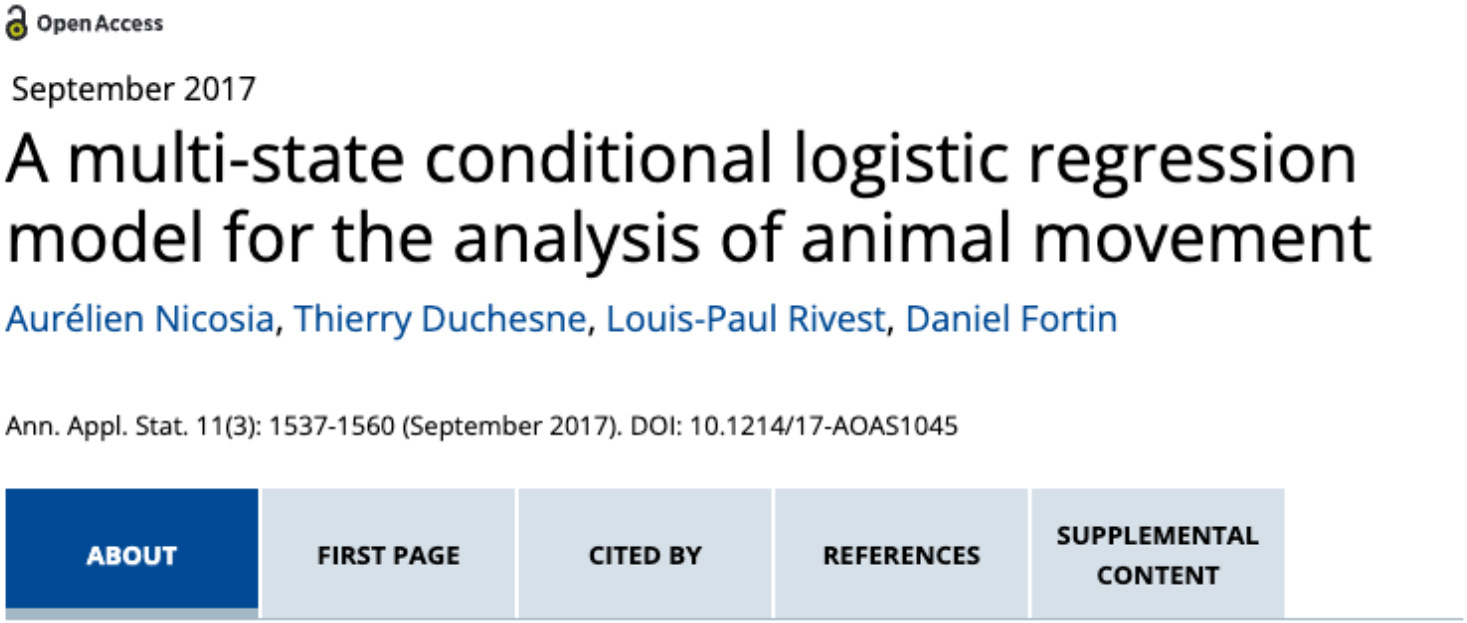
RESEARCH ARTICLE | Open Access

Behavioural state-dependent habitat selection and implications for animal translocations

Simona Picardi, Peter Coates, Jesse Kolar, Shawn O'Neil, Steven Mathews, David Dahlgren

First published: 12 November 2021 | https://doi.org/10.1111/1365-2664.14080 | Citations: 10

An integrated approach



Open Access

September 2017

A multi-state conditional logistic regression model for the analysis of animal movement

Aurélien Nicosia, Thierry Duchesne, Louis-Paul Rivest, Daniel Fortin

Ann. Appl. Stat. 11(3): 1537-1560 (September 2017). DOI: 10.1214/17-AOAS1045

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An integrated approach

Methodology | Open access | Published: 03 June 2023

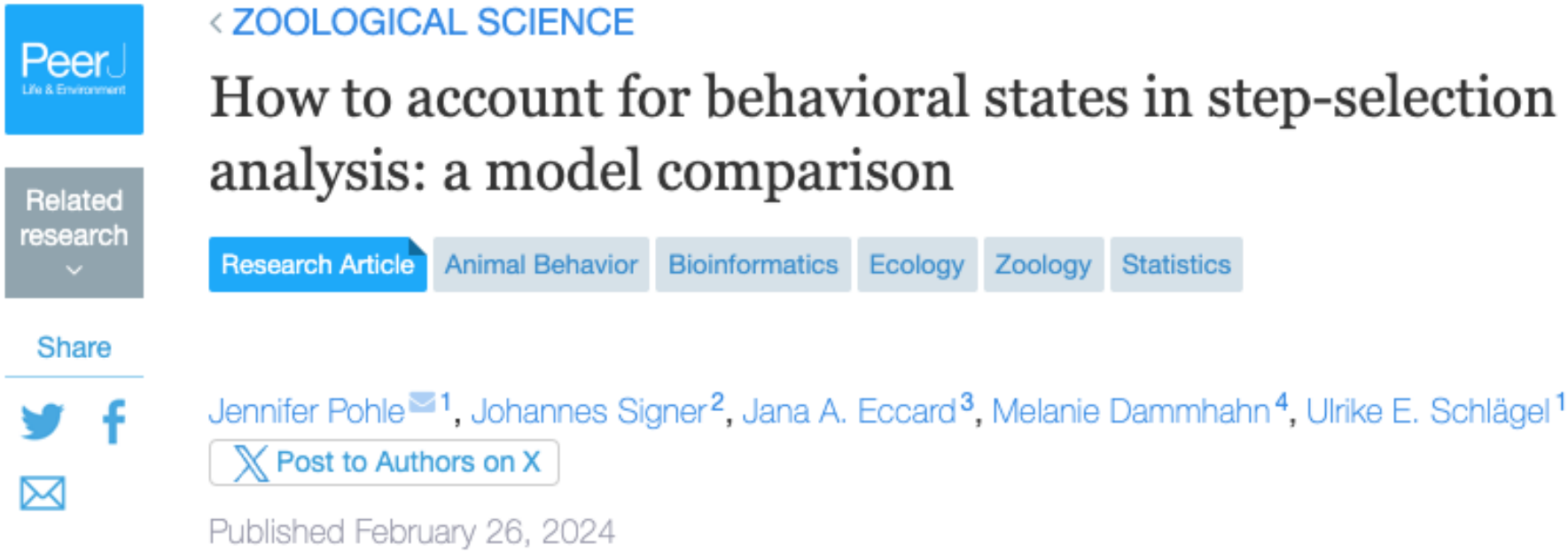
Flexible hidden Markov models for behaviour-dependent habitat selection

N. J. Klappstein ✉, L. Thomas & T. Michelot

Movement Ecology **11**, Article number: 30 (2023) | Cite this article

2447 Accesses | **2** Citations | **52** Altmetric | Metrics

An integrated approach



The idea is to simultaneously fit a Markov-switching variant of the conditional logistic regression:

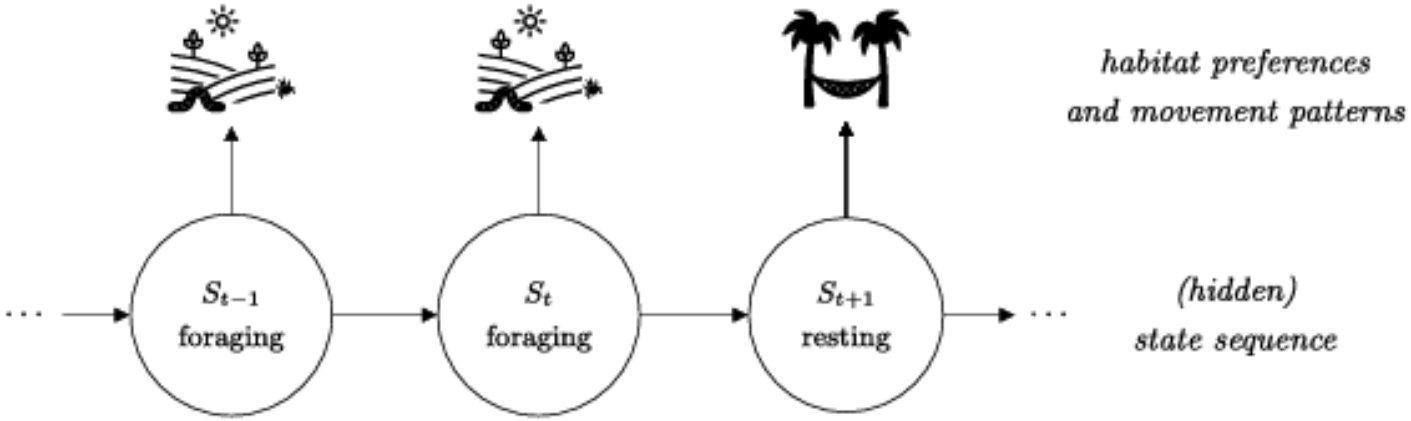
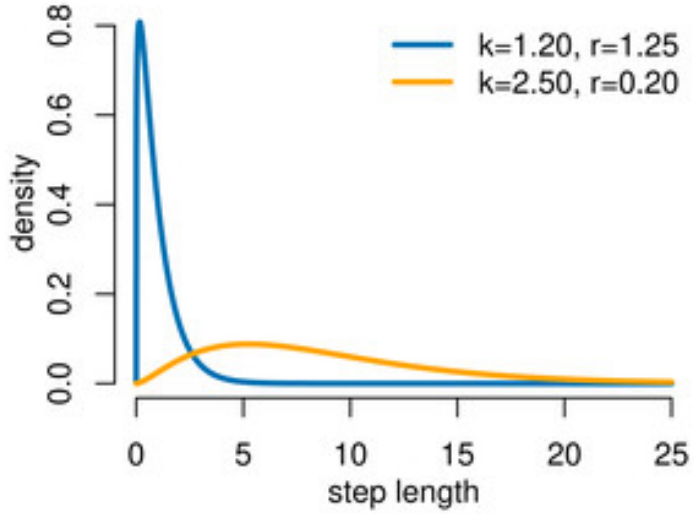
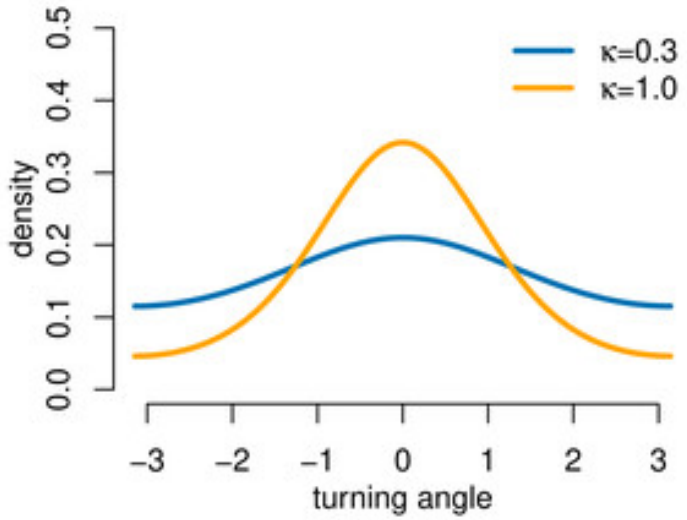


Figure 2: From Pohle et al. 2024

We can estimate different selection-free movement kernels and state-specific selection parameters without knowing the (hidden) covariate that separates states.





Irregular sampling rates

In a recent preprint Hofmann et al. compared 4 approaches:

Methodology | Open access | Published: 09 May 2024

Methods for implementing integrated step-selection functions with incomplete data

David D. Hofmann ✉, Gabriele Cozzi & John Fieberg

Movement Ecology **12**, Article number: 37 (2024) | Cite this article

Methodology | Open access | Published: 09 May 2024

Methods for implementing integrated step-selection functions with incomplete data

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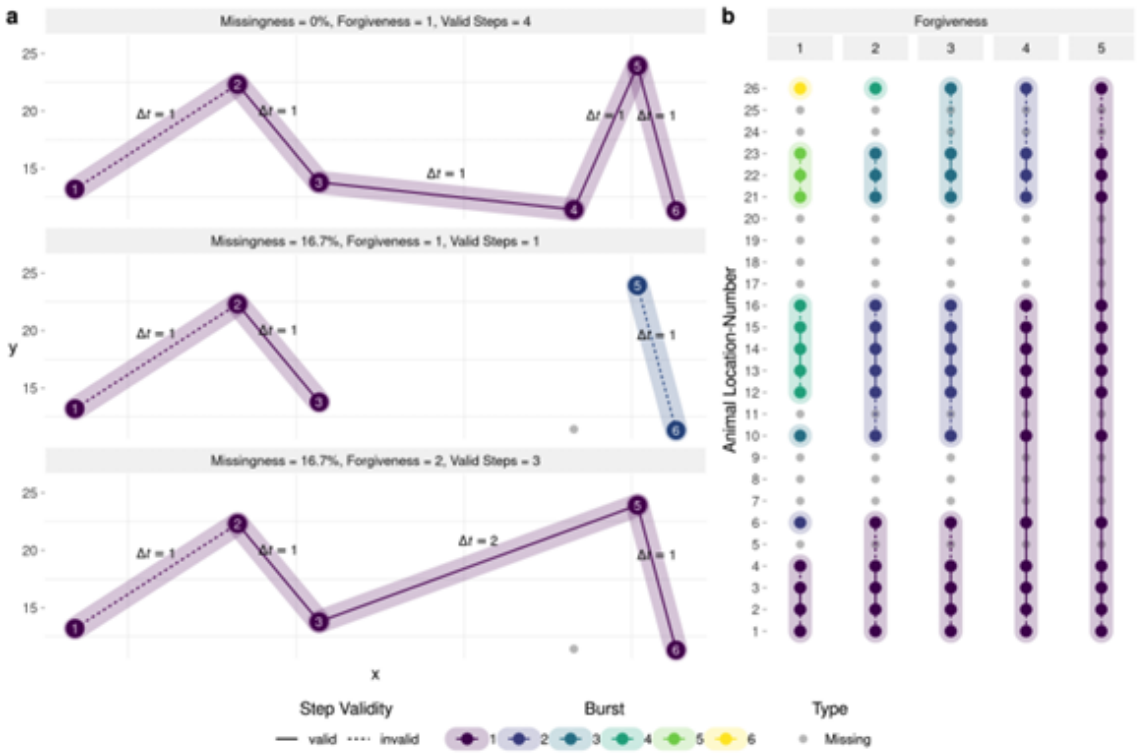
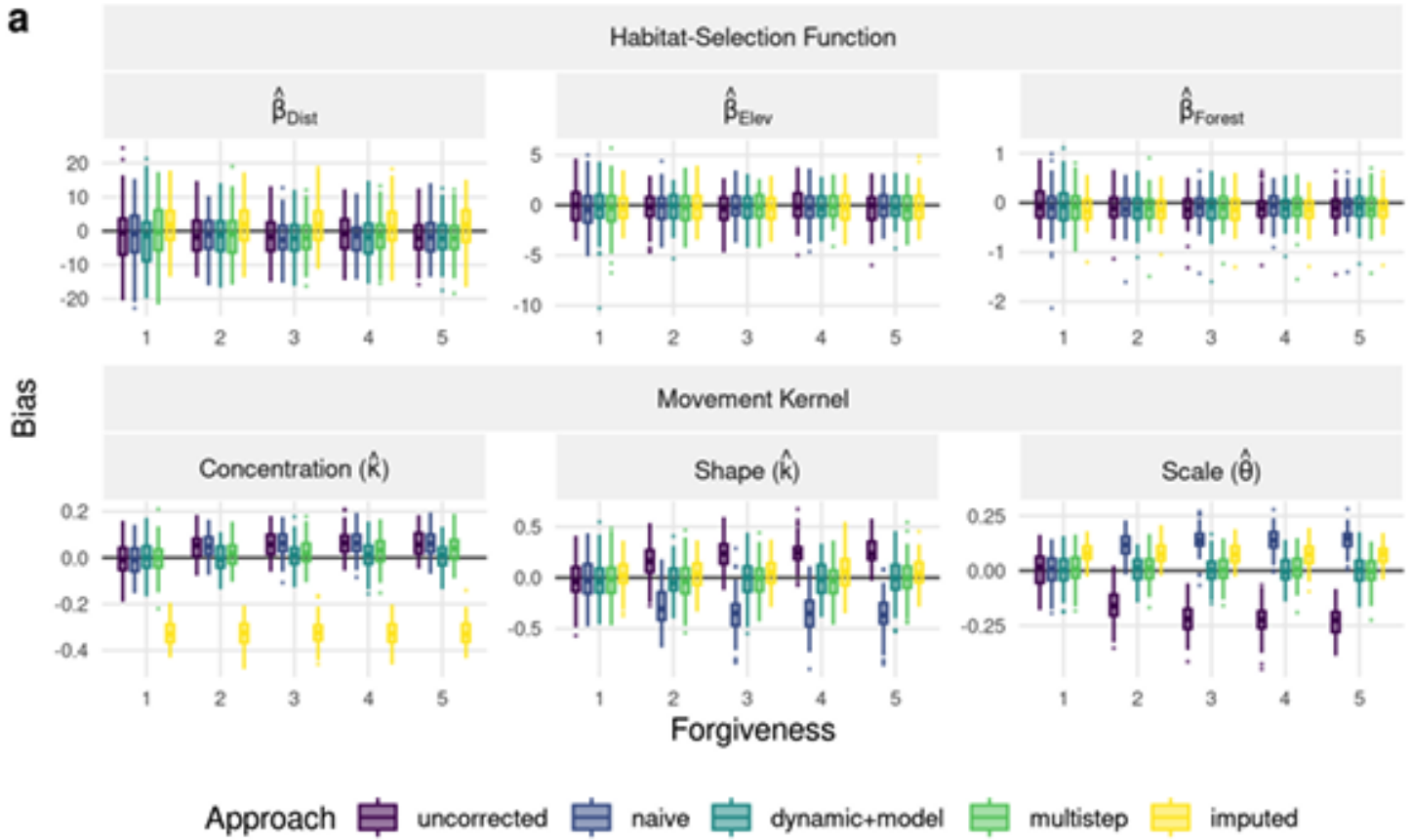
2688 Accesses | Metrics

1. Imputation using the `crawl` package.
2. Naive: Following a suggestion Munden et al. 2021 to find turning points and also model duration.
3. Dynamic+Model: Sample random steps from different tentative distributions.
4. Multistep: Using multiples of initial step length

Forgiveness: The maximum step-duration, measured in multiples of the regular step-duration, a modeler is willing to include in the step-selection analysis.



They then did a simulation study and compared the four approaches:



Account for non-linear relationships

- Effects do not have to be linear.
- We can use splines to model non-linearity.

Received: 12 January 2024 | Accepted: 21 May 2024

DOI: 10.1111/2041-210X.14367

Methods in Ecology and Evolution Open Access BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Step selection functions with non-linear and random effects

Natasha J. Klappstein[1] | Théo Michelot[1] | John Fieberg[2] | Eric J. Pedersen[3] | Joanna Mills Flemming[1]

Account for non-linear relationships

- Effects do not have to be linear.
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