Extensions to ‘classical’ iSSF

Johannes Signer

January 2024

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

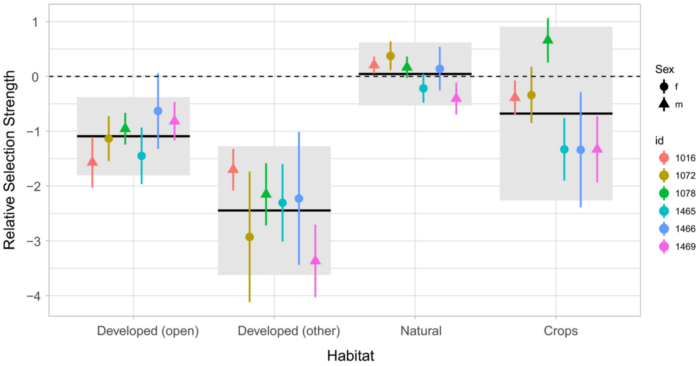

Figure 1: Source Signer et al. 2019

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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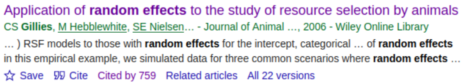

Application of **random effects** to the study of resource selection by animals
CS **Gillies**, M Hebblewhite, SE Nielsen… - Journal of Animal …, 2006 - Wiley Online Library
…) RSF models to those with **random effects** for the intercept, categorical … of **random effects** in this empirical example, we simulated data for three common scenarios where **random effects** …
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- 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.

Journal of Animal Ecology

BRITISH ECOLOGICAL SOCIETY

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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

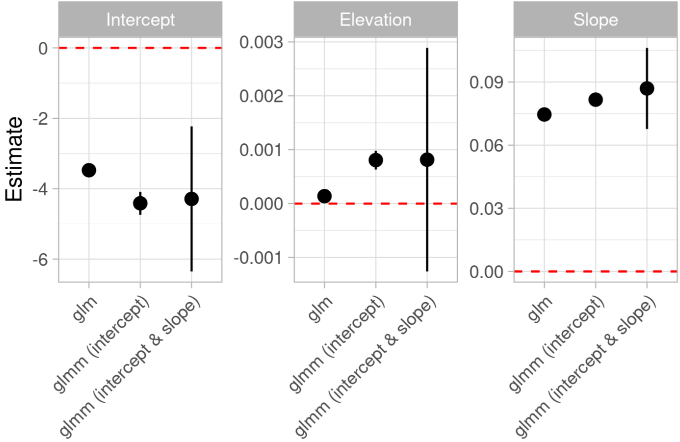
- Data on habitat selection of Mountain Goats[3]
- Generalized linear model with binomial response (GLM), random intercept (GLMM 1), and random intercept and slopes (GLMM 2).

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

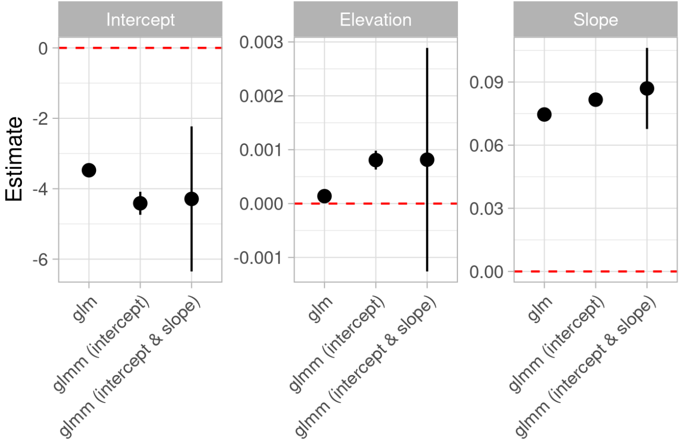
Let us fit three models to tracking data from wild goats:

```
# 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:



Comparing the model coefficients:



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

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]

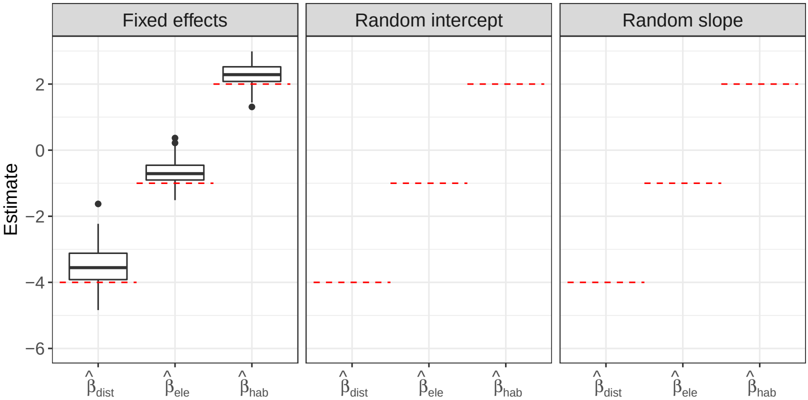
$$E(y_{nti}) = \mu_{nti} = \exp(\alpha_{nt} + \boldsymbol{\beta}^\top \boldsymbol{x}_{nti} + \boldsymbol{u}^\top \boldsymbol{z}_{nti}) \ , \quad y_{nti} \sim \text{Po}(\mu_{nti})$$

- $\alpha_{nt} \sim N(0, \sigma_\alpha^2)$ 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.

Simulation study from Muff et al. 2020

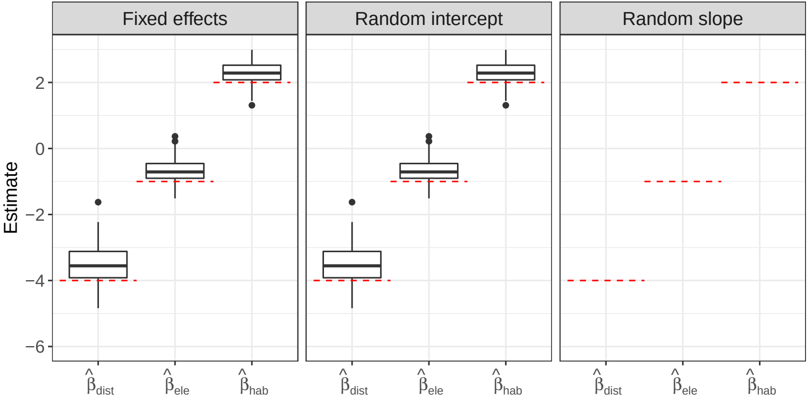
- Simulation of movement for 20 animals with animal-specific selection coefficients.
- For RSFs sample random points within the availability domain

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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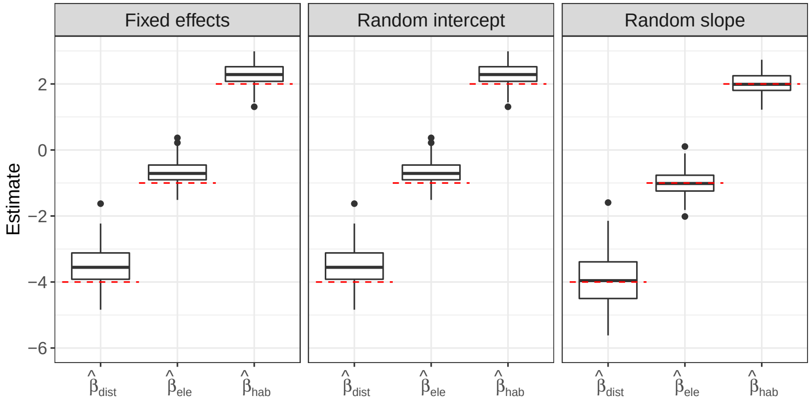
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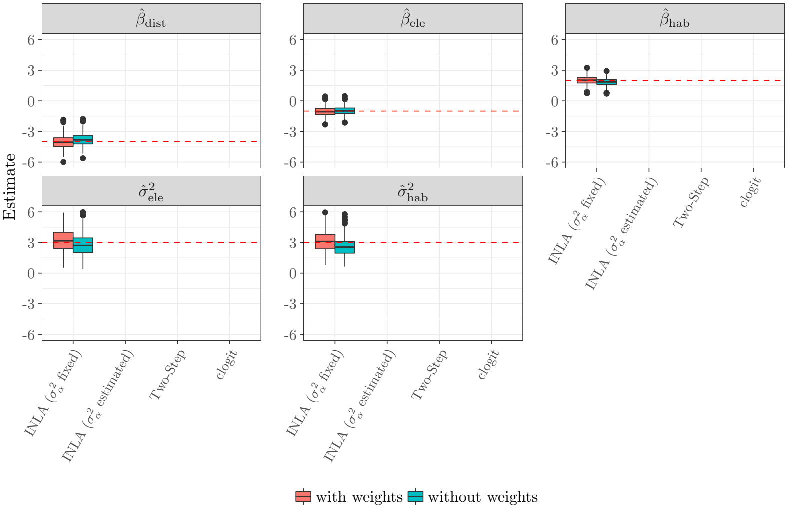
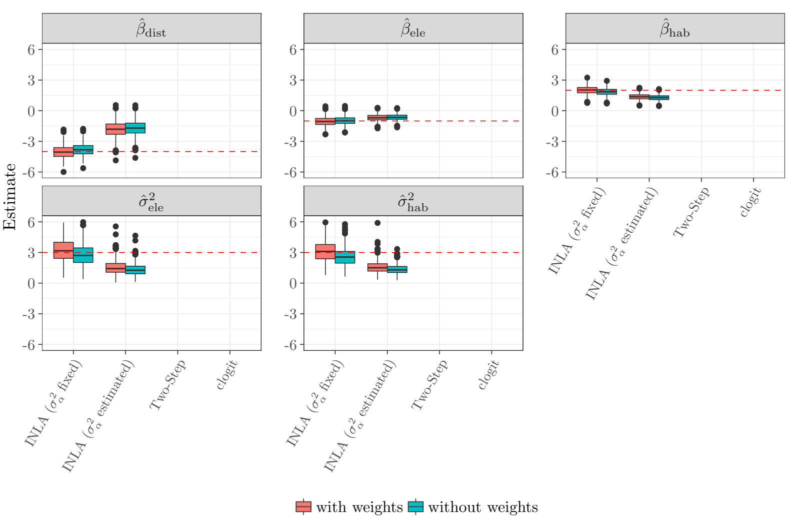


$\hat{\beta}_{\text{dist}}$
$\hat{\beta}_{\text{ele}}$
$\hat{\beta}_{\text{hab}}$
$\hat{\sigma}^2_{\text{ele}}$
$\hat{\sigma}^2_{\text{hab}}$
Estimate
6
3
0
-3
-6
INLA (σ^2_α fixed)
INLA (σ^2_α estimated)
Two-Step
clogit
with weights
without weights

Results SSF



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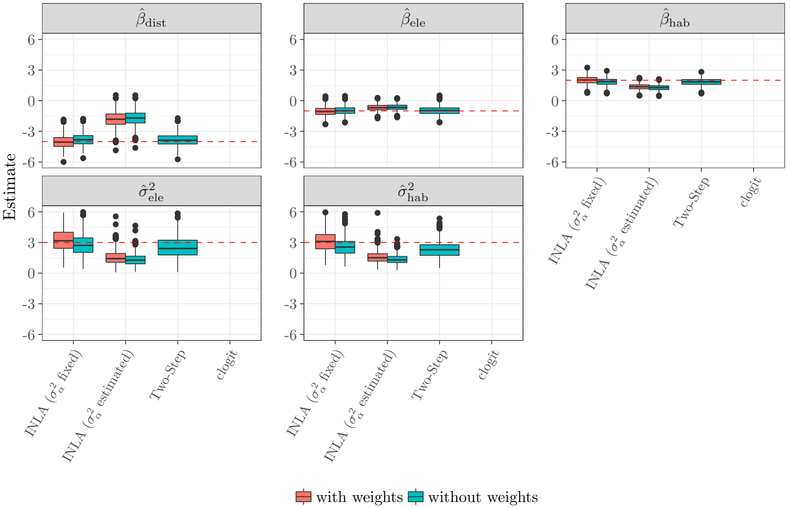

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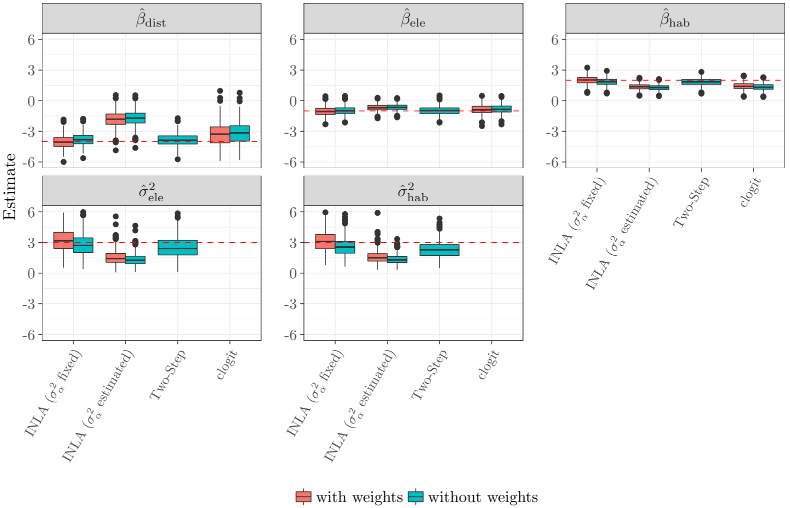

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Software to fit these models

- 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.

An example from Roshier et al. 2021

- This work I did together with David Roshier from Australian Wildlife Conservancy.
- I was only involved in the statistical modeling.

Received: 23 March 2021 | Revised: 31 May 2021 | Accepted: 3 June 2021
DOI: 10.1002/ece3.7810

ORIGINAL RESEARCH

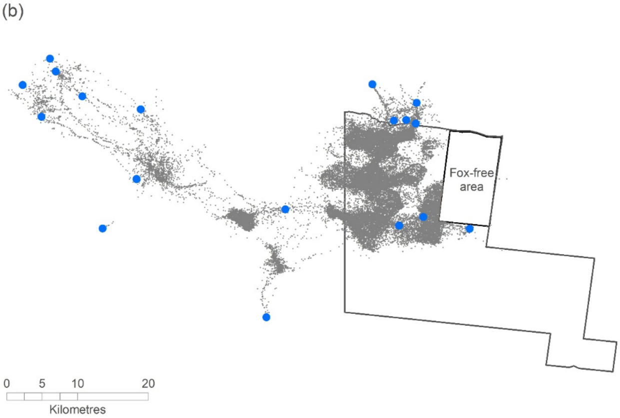
Ecology and Evolution Open Access WILEY

Visitation of artificial watering points by the red fox (*Vulpes vulpes*) in semiarid Australia

David A. Roshier[1,2] | Johannes Signer[3] | Andrew Carter[1,4]

Data

- Telemetry data for 22 individual foxes at 20 min sampling rate
- Location of water sources (in blue)



Analysis

1. Revisitation rates with the `recurse` package[1]
2. aKDE home ranges
3. integrated step selection analysis

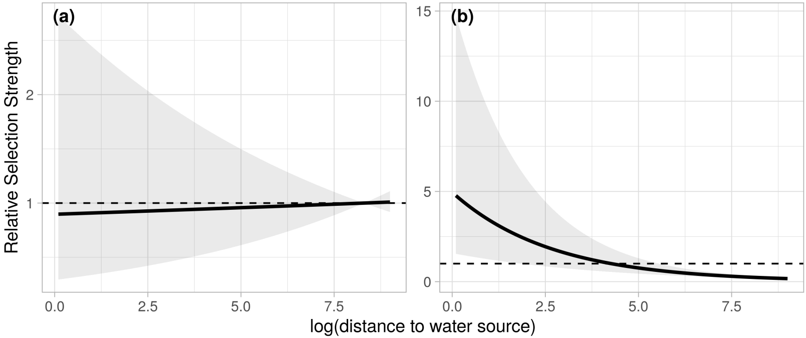
[1] Bracis, C., Bildstein, K. L., & Mueller, T. (2018). Revisitation analysis uncovers spatio-temporal patterns in animal movement data. Ecography, 41(11), 1801-1811.

Questions: iSSA

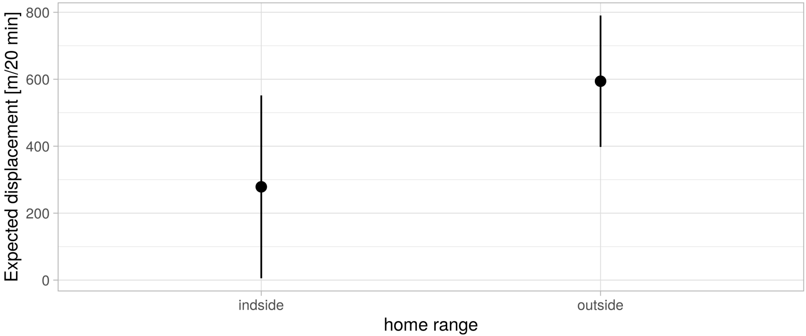
- Do foxes select for pixels closer to water sources?
- Does the selection depends on whether or not foxes are inside their home range?
- Do foxes move faster/slower when inside/outside their home range?

Habitat selection

Habitat selection of foxes inside (a) and outside (b) of their home range.



Expected displacement (i.e., how far do we expect a ‘typical’ fox to travel within a 20 minutes).



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

An integrated approach

How to account for behavioural states in step-selection analysis: a model comparison

J. Pohle[1]*, J. Signer[2], J. A. Eccard[3], M. Dammhahn[4] and U. E. Schlägel[1]

[1]Institute of Biochemistry and Biology, University of Potsdam, Potsdam, Germany
[2]Wildlife Sciences; Faculty of Forest Sciences and Forest Ecology; University of Goettingen, Göttingen, Germany
[3]Animal Ecology, University of Potsdam, Potsdam, Germany
[4] Behavioural Biology, University of Münster, Münster, Germany

Abstract

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

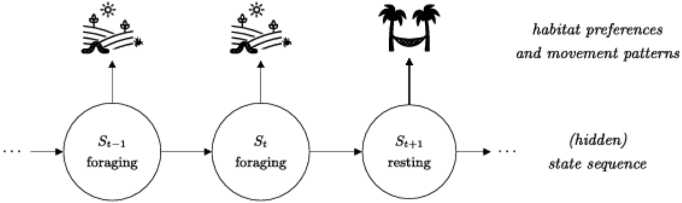
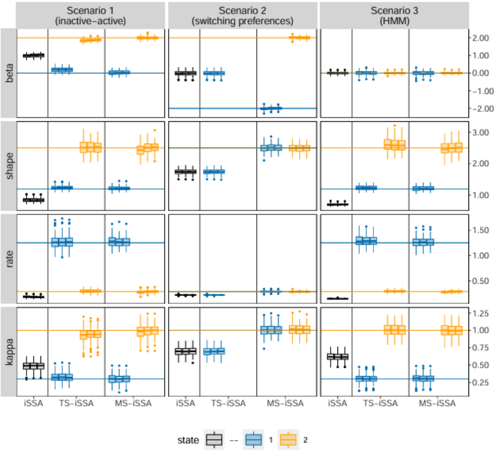


Figure 2: From Pohle et al. 2023

A simulation study was done by Pohle et al. 2023



Irregular sampling rates

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

Cold Spring Harbor Laboratory

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New Results

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Methods for Implementing Integrated Step-Selection Functions with Incomplete Data

David D. Hofmann, Gabriele Cozzi, John Fieberg

doi: https://doi.org/10.1101/2023.11.08.566194

This article is a preprint and has not been certified by peer review [what does this mean?].

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Methods for Implementing Integrated Step-Selection Functions with Incomplete Data

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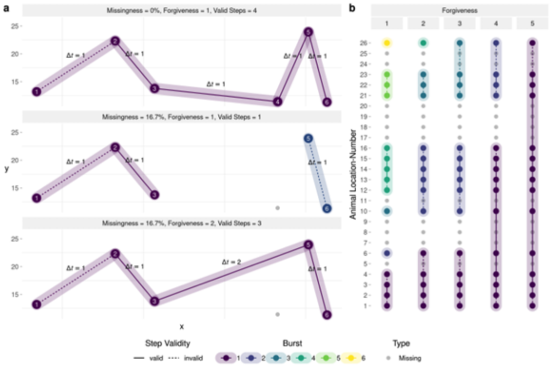
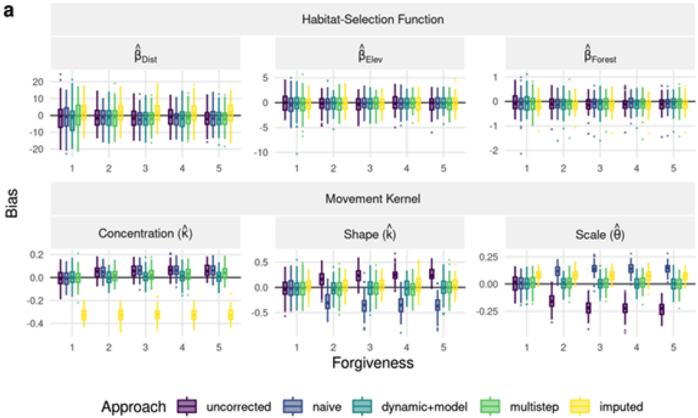
0 0 0 1 0 0 4

1. Imputation using the `crawl` package.
2. Naive: Following Munden et al. 2021
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

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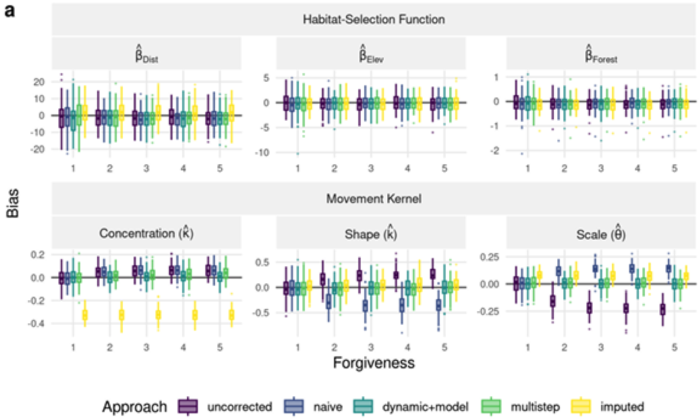
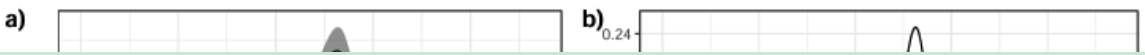


Account for non-linear relationships



Key resources/publications

- Muff, S., Signer, J., & Fieberg, J. (2020). Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. Journal of Animal Ecology, 89(1), 80-92.
- Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: overconfident estimates in mixed models. Behavioral ecology, 20(2), 416-420.