

How to Deal with Multiple Animals

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November 2022



Why should we care?

- Most telemetry studies consist of many animals.
- Often individual behave very differently (and we can fully account for these differences in a model).
- We are often interested in population-level effects.

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.

Resource Selection Function

- Global availability (unmatched)
- (weighted) Logistic regression¹

Step-Selection Function

- Availability conditioned on current position (matched)
- Conditional logistic regression

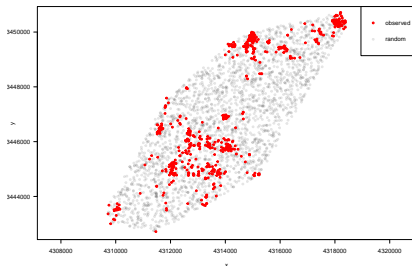
¹Fithian & Hastie. "Finite-sample equivalence in statistical models for presence-only data." The annals of applied statistics 7.4 (2013): 1917.

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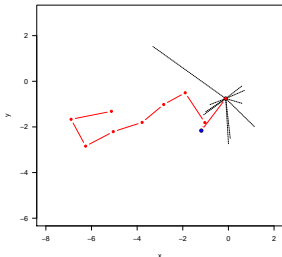
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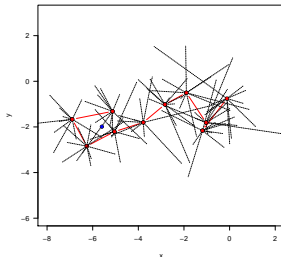
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2. Fit an individual model for each individual.

- 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

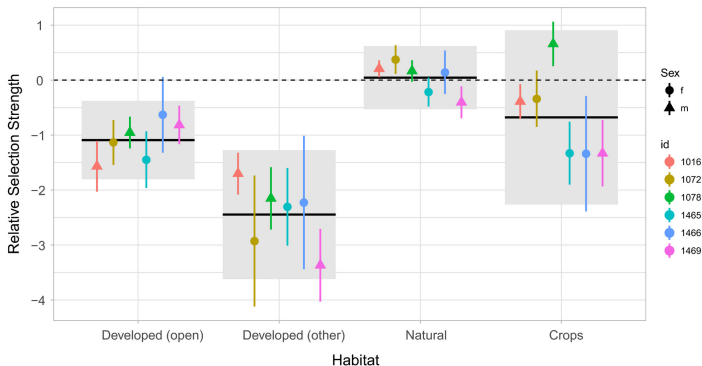


Figure 1: Source Signer et al. 2019

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 ago²

²Gillies 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
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...) 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).

²Gillies 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



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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 Goats³
- Generalized linear model with binomial response (GLM), random intercept (GLMM 1), and random intercept and slopes (GLMM 2).

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

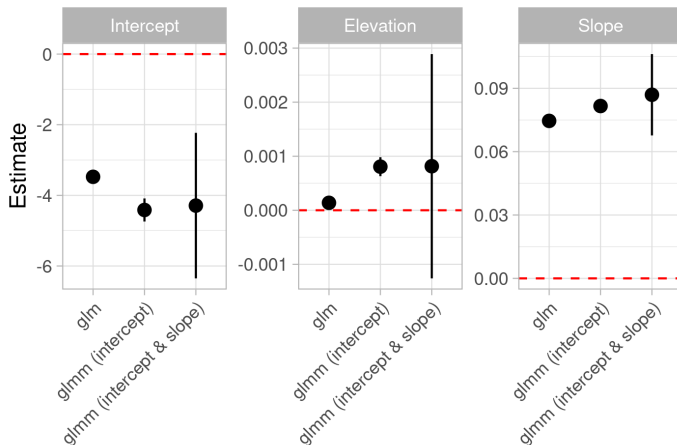
Let us fit three models to tracking data from wild goats:

```
# 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())

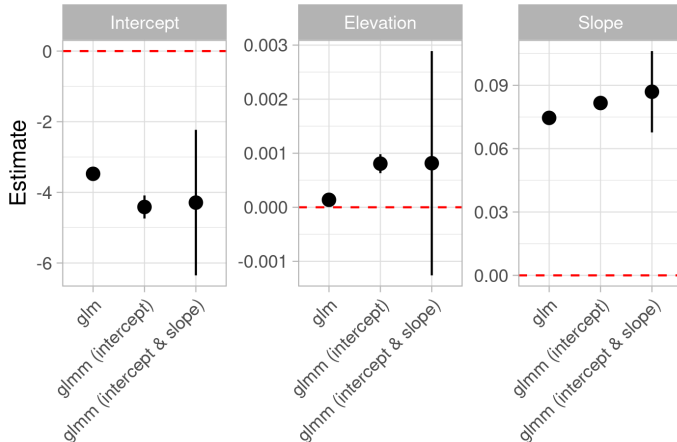
# This is a random slope and intercept model
m3 <- glmmTMB(STATUS ~ ELEVATION + SLOPE +
              (ELEVATION + SLOPE | ID),
              data = goats, family = binomial())
```


Comparing the model coefficients:



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

Comparing the model coefficients:



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

⁴Schielzeth, & 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

$$P(y_{ntj} = 1 | \mathbf{x}_{nt\cdot}) = \pi_{ntj} = \frac{\exp(\boldsymbol{\beta}^\top \mathbf{x}_{ntj})}{\sum_{j=1}^J \exp(\boldsymbol{\beta}^\top \mathbf{x}_{nti})}$$

- $n = 1, \dots, N$ individuals, with realized steps,
- time points $t = 1, \dots, T_n$, with
- $j = 1, \dots, J_{n,t}$ location that were either used or available.

- 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}

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

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

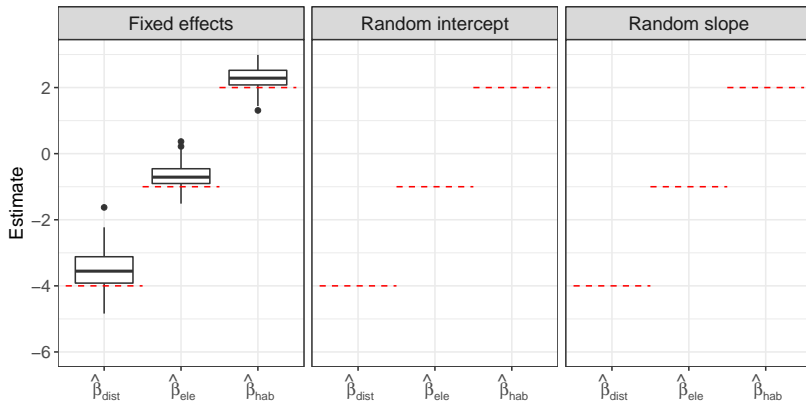
⁵Armstrong et al. "Conditional Poisson models: a flexible alternative to conditional logistic case cross-over analysis." BMC medical research methodology 14.1 (2014): 122.

⁶Muff, 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.

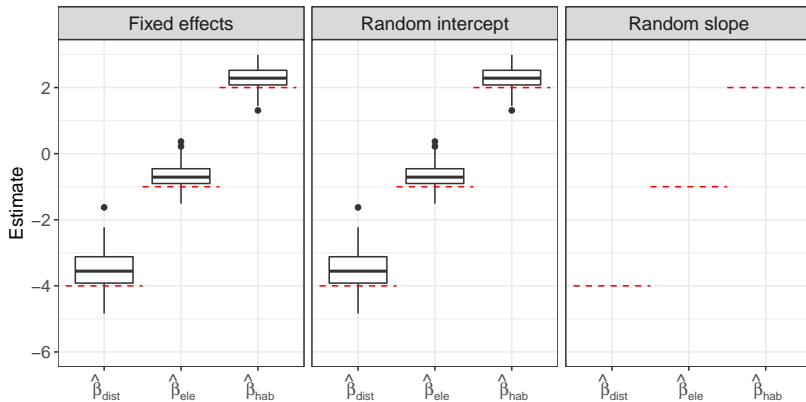
Simulation study from Muff et al. 2020

- 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

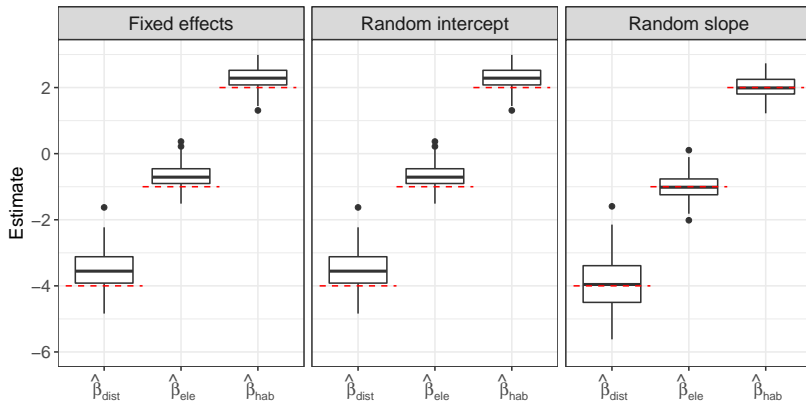
Results HSF



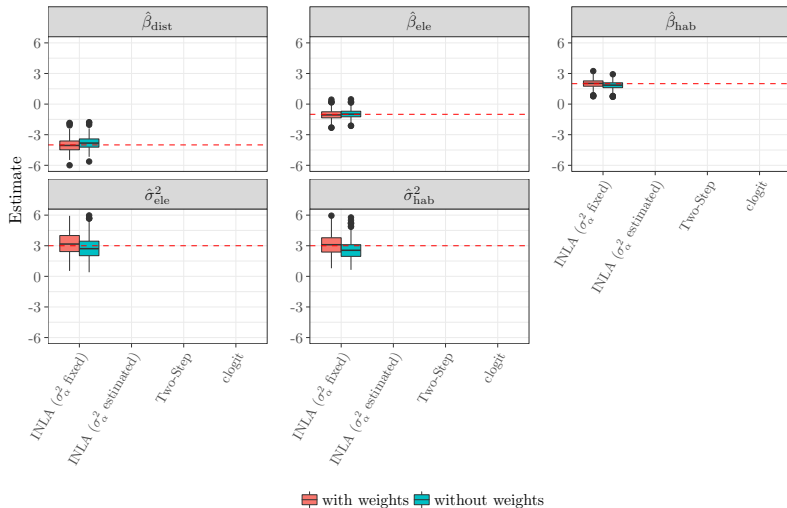
Results HSF



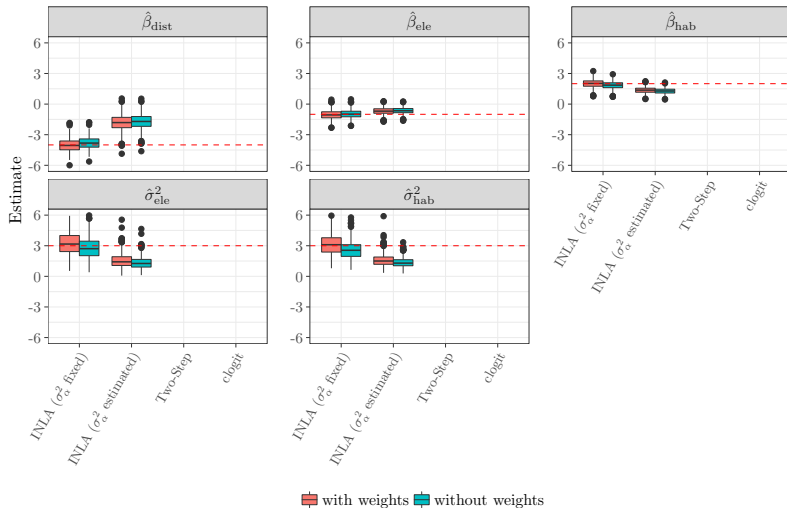
Results HSF



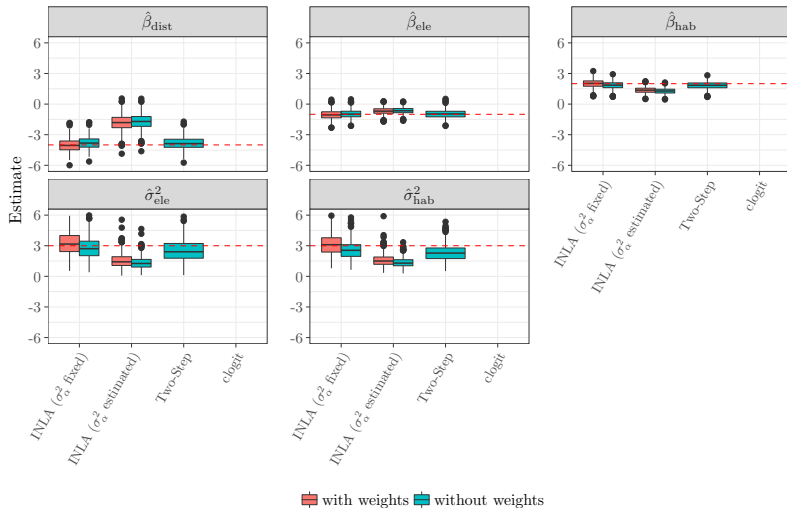
Results SSF



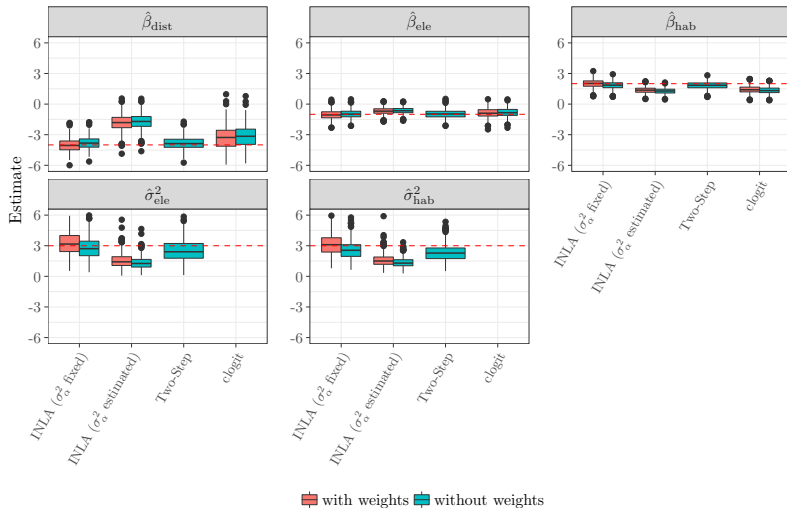
Results SSF



Results SSF



Results SSF



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

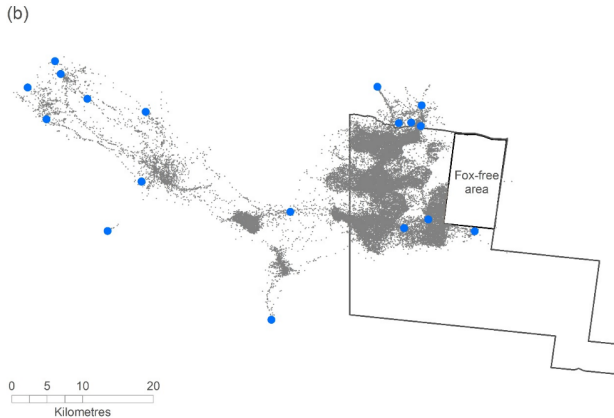
Ecology and Evolution  WILEY

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

David A. Roshier^{1,2}  | Johannes Signer³ | 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 package¹
2. aKDE home ranges
3. integrated step selection analysis

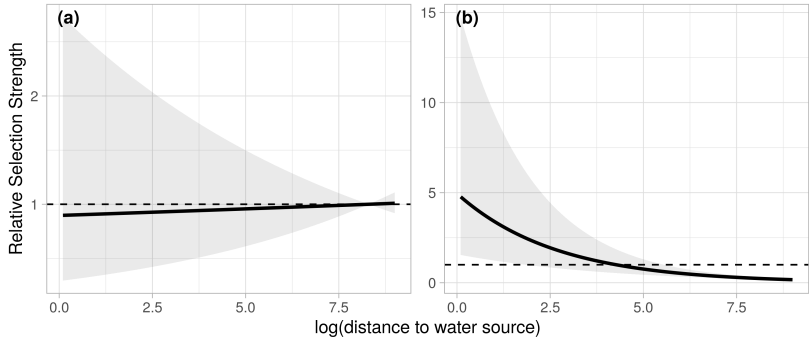
¹Bracis, C., Bildstein, K. L., & Mueller, T. (2018). Revisitation analysis uncovers spatio-temporal patterns in animal movement data. *Ecography*, 41(11), 1801-1811.

Questions: iSSA

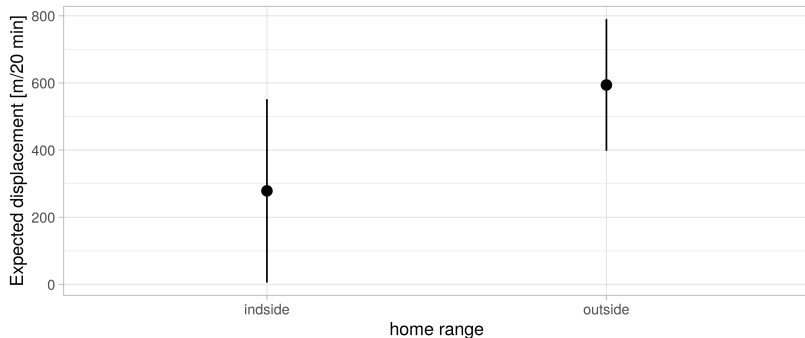
- Do foxes select for pixels closer to water sources?
- Does the selection depends on whether or not foxes are inside their home range?
- Do foxes move faster/slower when inside/outside their home range?

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).



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.