Methods for modeling variability among-animals in habitat-selection studies

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BIOLOGGING

Journal of Animal Ecology

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

Stefanie Muff[1,2] | Johannes Signer[3] | John Fieberg[4]

Outline

- Motivation for studying variability among-animals
- Methods for modeling variability among-animals
  - 2-step methods
  - Mixed-effects models

Causes and consequences of among-animal variability

Methods for modeling among-animal variability

Causes of Individual Variability

Volume 26, Issue 2
March-April 2015

Sex-specific adjustments in habitat selection contribute to buffer mouflon against summer conditions FREE

Pascal Marchand, Mathieu Garel, Gilles Bourgoin, Dominique Dubray, Daniel Maillard, Anne Loison Author Notes

Behavioral Ecology, Volume 26, Issue 2, 1 March 2015, Pages 472–482,
https://doi.org/10.1093/beheco/aru212

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Received: 22 August 2016 | Revised: 12 December 2016 | Accepted: 22 December 2016
DOI: 10.1002/ece3.2764

ORIGINAL RESEARCH

WILEY Ecology and Evolution

Complex variation in habitat selection strategies among individuals driven by extrinsic factors

Edward J. Raynor[1] | Hawthorne L. Beyer[2] | John M. Briggs[1] | Anthony Joern[1]

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[2]ARC Centre of Excellence for Environmental Decisions, The University of Queensland, Brisbane, Qld, Australia

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Edward J. Raynor, School of Natural Resources, University of Nebraska, Lincoln, NE, USA

Funding information
Division of Environmental Biology; National Science Foundation (NSF), Grant/Award Number: DEB 1020485; NSF Konza LTER.

Abstract
Understanding behavioral strategies employed by animals to maximize fitness in the face of environmental heterogeneity, variability, and uncertainty is a central aim of animal ecology. Flexibility in behavior may be key to how animals respond to climate and environmental change. Using a mechanistic modeling framework for simultaneously quantifying the effects of habitat preference and intrinsic movement on space use at the landscape scale, we investigate how movement and habitat selection vary among individuals and years in response to forage quality–quantity tradeoffs, environmental conditions, and variable annual climate. We evaluated the association of dynamic, biotic forage resources and static, abiotic landscape features with large grazer movement decisions in an experimental landscape, where forage resources vary in response to prescribed burning, grazing by a native herbivore, the plains bison (*Bison bison bison*), and a continental climate. Our goal was to determine how biotic and abiotic factors mediate bison movement decisions in a nutritionally heterogeneous grassland. We integrated spatially explicit relocations of GPS-collared bison and extensive vegetation surveys to relate movement paths to grassland attributes over a time pe-

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Evolutionary Ecology
March 1989, Volume 3, Issue 1, pp 80–94 | Cite as

Density-dependent habitat selection: Testing the theory with fitness data

Authors Authors and affiliations

Douglas W. Morris

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Habitat selection by predators and prey in communities with asymmetrical intraguild predation

Michael R. Heithaus

Heithaus, M. R. 2001. Habitat selection by predators and prey in communities with asymmetrical intraguild predation. – Oikos 92: 542–554.

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Habitat selection by predators asymmetrical intraguild predati

Michael R. Heithaus

Heithaus, M. R
asymmetrical ir

GENETIC VARIATION FOR HABITAT PREFERENCE: EVIDENCE AND EXPLANATIONS

John Jaenike and Robert D. Holt

Department of Biology, University of Rochester, Rochester, New York 14627;
Museum of Natural History and Department of Systematics and Ecology,
University of Kansas, Lawrence, Kansas 66045

Abstract.—Because adaptive shifts may often be initiated by evolutionary changes in behavior, it is of interest to determine the extent to which natural populations harbor genetic variation for ecologically important behaviors. Habitat preference is an especially significant behavior, because it determines the regime of natural selection acting on loci that affect adaptation to the environment. A survey of the literature reveals that genetic variation for habitat selection is common, especially in arthropods and mollusks, the groups that have been studied most frequently. Possible adaptive mechanisms by which this variation could be maintained within populations include a genetic correlation between density-independent fitness in a habitat and a preference for it; and soft selection, whereby density-dependent population regulation occurs independently in separate habitats. Several studies have documented a phenotypic correlation

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Why do we care about individual variability?

Both Environment and Genetic Makeup Influence Behavior

By: Michael D. Breed (*Department of Ecology & Evolutionary Biology, University of Colorado at Boulder*) & Leticia Sanchez (*Department of Ecology & Evolutionary Biology, University of Colorado at Boulder*) © 2010 Nature Education

Citation: Breed, M. & Sanchez, L. (2010) Both Environment and Genetic Makeup Influence Behavior. *Nature Education Knowledge* 3(10):68

How do genes and the environment come together to shape animal behavior? Both play important roles. Genes capture the evolutionary responses of prior populations to selection on behavior. Environmental flexibility gives animals the opportunity to adjust to changes during their own lifetime.

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50 YEARS WITH IMPACT Journal of Applied Ecology

Journal of Applied Ecology 2015, **52**, 496–504 doi: 10.1111/1365-2664.12400

Adjustments in habitat selection to changing availability induce fitness costs for a threatened ungulate

Chrystel L. Losier[1,2], Serge Couturier[1], Martin-Hugues St-Laurent[2,3,4], Pierre Drapeau[2,5], Claude Dussault[6], Tyler Rudolph[2,5], Vincent Brodeur[7], Jerod A. Merkle[1,2] and Daniel Fortin[1,2]*

[1]Chaire de recherche industrielle CRSNG – Université Laval en sylviculture et faune, Département de biologie, Université Laval, Québec, QC G1V 0A6, Canada; [2]Centre d'étude de la forêt, 2405 rue de la Terrasse, Québec, QC G1V 0A6, Canada; [3]Département de Biologie, Chimie et Géographie, Université du Québec à Rimouski, Rimouski, QC G5L 3A1, Canada; [4]Centre d'études nordiques, 2405 rue de la Terrasse, Québec, QC G1V 0A6, Canada; [5]Chaire de recherche industrielle CRSNG – Université du Québec en Abitibi-Témiscamingue et Université du Québec à Montréal en aménagement forestier durable, Département des sciences biologiques, Université du Québec à Montréal, Montréal, QC H3C 3P8, Canada; [6]Ministère du Développement durable, de l'Environnement de la Faune et des Parcs, Directeur régional par intérim du Saguenay – Lac-St-Jean, 3950 boul. Harvey, Jonquière, QC G7X 8L6, Canada; and [7]Ministère du Développement durable, de l'Environnement de la Faune et des Parcs, Direction des opérations régionales du Nord-du-Québec, 951 boul. Hamel, Chibougamau, QC G8P 2Z3, Canada

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ECOLOGY LETTERS

Ecology Letters, (2018) 21: 665–673 doi: 10.1111/ele.12933

LETTER

Intragroup competition predicts individual foraging specialisation in a group-living mammal

Catherine E. Sheppard,[1] Richard Inger,[2] Robbie A. McDonald,[2] Sam Barker,[2] Andrew L. Jackson,[3] Faye J. Thompson,[1] Emma I. K. Vitikainen,[1,4] Michael A. Cant[1]* and Harry H. Marshall[1,5]*

Abstract

Individual foraging specialisation has important ecological implications, but its causes in grou living species are unclear. One of the major consequences of group living is increased intragro competition for resources. Foraging theory predicts that with increased competition, individu should add new prey items to their diet, widening their foraging niche ('optimal foraging hypot sis'). However, classic competition theory suggests the opposite: that increased competition lea to niche partitioning and greater individual foraging specialisation ('niche partitioning hypothesis We tested these opposing predictions in wild, group-living banded mongooses (*Mungos mung* using stable isotope analysis of banded mongoose whiskers to quantify individual and group fo aging niche. Individual foraging niche size declined with increasing group size, despite all grou having a similar overall niche size. Our findings support the prediction that competition promo niche partitioning within social groups and suggest that individual foraging specialisation m play an important role in the formation of stable social groupings.

Keywords

Banded mongoose, competition, foraging behaviour, foraging niche, group-living, *Mungos mung* social group, specialisation, stable isotope.

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50 YEARS WITH IMPACT — Journal of Applied Ecology — British Ecological Society

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PNAS

Food limitation leads to behavioral diversification and dietary specialization in sea otters

M. Tim Tinker*[†], Gena Bentall[‡], and James A. Estes[§]

*Department of Ecology and Evolutionary Biology, University of California, Center for Ocean Health, 100 Shaffer Road, Santa Cruz, CA 95060; [‡]Sea Otter Research and Conservation, Monterey Bay Aquarium, 886 Cannery Row, Monterey, CA 93940; and [§]U.S. Geological Survey, Western Ecological Research Center, Long Marine Laboratory, 100 Shaffer Road, Santa Cruz, CA 95060

Edited by Robert T. Paine, University of Washington, Seattle, WA, and approved November 28, 2007 (received for review September 28, 2007)

Dietary diversity often varies inversely with prey resource abundance. This pattern, although typically measured at the population level, is usually assumed to also characterize the behavior of individual animals within the population. However, the pattern might also be produced by changes in the degree of variation among individuals. Here we report on dietary and associated behavioral changes that occurred with the experimental translo-

their prey, and we have obtained longitudinal records of sea otter diet and foraging behavior from tagged individuals that span multiple years (8). Moreover, the experimental translocation of sea otters from central California (henceforth CC) to San Nicolas Island (henceforth SN) in the southern California Bight in 1987–1990 established a second population in a comparatively food-rich environment where the diversity of potential inverte-

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ECOLOG

Ecology Letters, (2018) 21: 665–6

LETTER

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Ecology Letters (2018) 21: 665–673

Oecologia (2017) 185:415–425
DOI 10.1007/s00442-017-3939-8

CrossMark

BEHAVIORAL ECOLOGY –ORIGINAL RESEARCH

Not accounting for interindividual variability can mask habitat selection patterns: a case study on black bears

Rémi Lesmerises[1] · Martin-Hugues St-Laurent[2]

PNAS

:ation

M. Tim Tinker*[†], Gena Bentall[‡], and James A. Estes[§]

*Department of Ecology and Evolutionary Biology, University of California, Center for Ocean Health, 100 Shaffer Road, Santa Cruz, CA 95060; [‡]Sea Otter Research and Conservation, Monterey Bay Aquarium, 886 Cannery Row, Monterey, CA 93940; and [§]U.S. Geological Survey, Western Ecological Research Center, Long Marine Laboratory, 100 Shaffer Road, Santa Cruz, CA 95060

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Understanding Functional Responses

Habitat selection parameters, β, are informed by habitat use relative to habitat availability.

- when $f^u(x) > f^a(x) \Rightarrow$ "preference" for habitat x.

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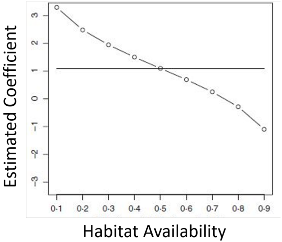

Aarts, G., Fieberg, J., Brasseur, S., & Matthiopoulos, J. (2013). Quantifying the effect of habitat availability on species distributions. Journal of animal ecology, 82(6), 1135-1145.

Ecology, 79(4), 1998, pp. 1435–1441

FUNCTIONAL RESPONSES IN HABITAT USE: AVAILABILITY INFLUENCES RELATIVE USE IN TRADE-OFF SITUATIONS

ATLE MYSTERUD AND ROLF ANKER IMS

Department of Biology, Division of Biology, P.O. Box 1050 Blindern, University of Oslo, N-0316 Oslo, Norway

Habitat-use patterns depend on:

- habitat availability and...
- interactions between different resources risks, and conditions

Individuals may spend more time feeding if resource rich patches are near areas with good escape cover.

Mysterud and Ims (1998)

- Developed an approach to modeling functional responses
- Limited to considering two discrete habitat types

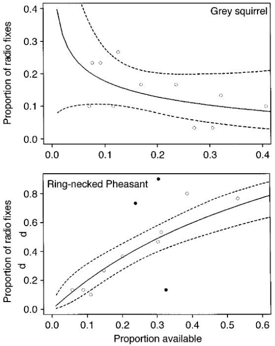

FIG. 1. Logistic regression of proportional use against proportion of that habitat available within an individual's home range for gray squirrel and Ring-necked Pheasants, with 95% confidence envelopes. Note that the regression for the Ring-necked Pheasant includes three misfitting observations (solid circles); thus the confidence envelopes may be underestimated.

Generalized Functional Responses

Ecology, 92(3), 2011, pp. 583–589

Generalized functional responses for species distributions

Jason Matthiopoulos,[1,2,7] Mark Hebblewhite,[3] Geert Aarts,[4,5] and John Fieberg[6]

[1]*Scottish Oceans Institute, School of Biology, University of St. Andrews, East Sands, St. Andrews, Fife KY16 8LB Scotland, United Kingdom*
[2]*Centre for Research into Environmental and Ecological Modeling, University of St Andrews, The Observatory, Buchanan Gardens, St Andrews, Fife KY16 9LZ Scotland, United Kingdom*
[3]*Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, College of Forestry and Conservation, University of Montana, Missoula, Montana 59812 USA*
[4]*Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, The Netherlands*
[5]*IMARES Wageningen UR, Institute for Marine Resources and Ecosystem Studies, P.O. Box 167, 1790 AD Den Burg, The Netherlands*
[6]*Biometrics Unit, Minnesota Department of Natural Resources (Minnesota DNR), 5463-C West Broadway, Forest Lake, Minnesota 55025 USA*

Capture variability in habitat-selection parameters (in RSFs) across multiple sampling instances using:

- moments of availability (mean, variance)
- interactions between these moments
- random coefficients

Causes and consequences of among-animal variability

Methods for modeling among-animal variability

Methods for modeling among-animal variability

1. Fit models to individual animals (or sampling instances) and treat the estimates as data (two-step approach)

2. Mixed models, hierarchical models, random-effect models: allow parameters to vary by animal

Two-Step Approach

Step 1: fit models to individuals

$$f_i^u(s) \propto \exp(x_1(s)\beta_{1i} + x_2(s)\beta_{2i} + \ldots x_p(s)\beta_{pi})$$

Two-Step Approach

Step 1: fit models to individuals

$$f_i^u(s) \propto \exp(x_1(s)\beta_{1i} + x_2(s)\beta_{2i} + \ldots x_p(s)\beta_{pi})$$

Step 2: Do statistics on $(\hat{\beta}_{1i}, \ldots, \hat{\beta}_{pi})$

Two-Step Approach

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Step 2: Do statistics on $(\hat{\beta}_{1i}, \ldots, \hat{\beta}_{pi})$

Covariates:

- elevation
- population density
- forest (yes/no)

Fieberg J, Bohrer G, Davidson SC, Kays R (2018) Short course on analyzing animal tracking data. Presented at the North Carolina Museum of Natural Sciences, Raleigh, NC, USA. May 21-23, 2018. https://movebankworkshopraleighnc.netlify.com/

LaPoint, S., Gallery, P., Wikelski, M., and Kays, R. 2013. Animal behavior, cost-based corridor models, and real corridors. Landscape Ecology, 28, 1615-1630.

amt: Individual-Specific Coefficients

Quick and easy using the `amt` package in conjunction with `tidyverse` in R

Fit models to individuals:

```
rsffits <- dat_rsf %>% nest(data=!c(id, sex)) %>%
  mutate(mod = map(data, function(x)
    glm(case_ ~ elevation + popden + forest,
        data = x, weight=w, family = binomial)))
```

Pull off coefficients:

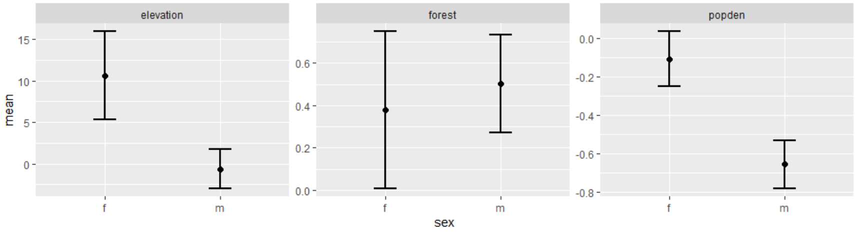
```
rsffits2 <- rsffits %>%
  dplyr::mutate(tidy = purrr::map(mod, broom::tidy),
                n = purrr::map(data, nrow) %>% simplify()) %>%
  unnest(tidy) %>% select(-c(data, mod))
```

Data Frame: Individual-Specific Coefficients

```
> rsffits2
# A tibble: 24 x 8
      id sex   term        estimate std.error statistic  p.value     n
   <dbl> <chr> <chr>          <dbl>     <dbl>     <dbl>    <dbl> <int>
 1     2 f     (Intercept)  -8.36      0.489    -17.1   1.33e-65 14828
 2     2 f     forest        1.02      0.0602    16.9   2.04e-64 14828
 3     2 f     elevation     1.64      0.524      3.13  1.75e- 3 14828
 4     2 f     popden        0.142     0.0777     1.83  6.73e- 2 14828
 5     4 f     (Intercept)   1.79      0.950      1.88  5.95e- 2 11132
 6     4 f     forest        0.160     0.0667     2.39  1.67e- 2 11132
 7     4 f     elevation    13.0       1.12      11.7   2.25e-31 11132
 8     4 f     popden       -0.260     0.0723    -3.60  3.22e- 4 11132
 9     5 f     (Intercept)   6.69      2.85       2.35  1.90e- 2  5599
10     5 f     forest       -0.0470    0.114     -0.412 6.80e- 1  5599
# ... with 14 more rows
>
```

Signer, J., J. Fieberg, and T. Avgar (2019). Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecology and Evolution 9:880-890.

Step 2: Statistics on Statistics



- relate coefficients to animal-specific characteristics (e.g., age, sex) using say `lm`

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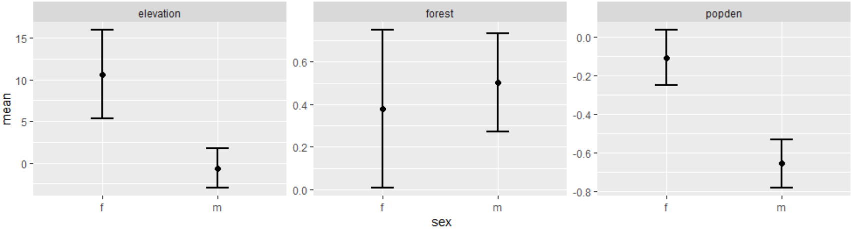
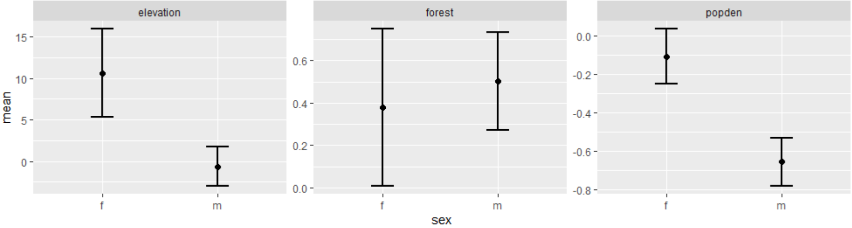


- relate coefficients to animal-specific characteristics (e.g., age, sex) using say `lm`
- calculate variance/covariance (biased high due to sampling variability)

Step 2: Statistics on Statistics



- relate coefficients to animal-specific characteristics (e.g., age, sex) using say `lm`
- calculate variance/covariance (biased high due to sampling variability)
- plot coefficients against availability to explore functional responses

Two-Step Approach

- Often a useful starting point (exploratory data analysis)

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In the context of step-selection functions:

- Craiu, R. V., T. Duchesne, D. Fortin, and S. Baillargeon (2011). Conditional logistic regression with longitudinal follow-up and individual-level random coefficients: A stable and efficient two-step estimation method. Journal of Computational and Graphical Statistics 20, 767-784.
- Craiu, R. V., T. Duchesne, D. Fortin, and S. Baillargeon (2016). TwoStepCLogit: Conditional Logistic Regression: A Two-Step Estimation Method. R package version 1.2.5.

Mixed-Effect Models

Contain fixed and random effects. What is the difference?

- random effects allow one to generalize to a larger population
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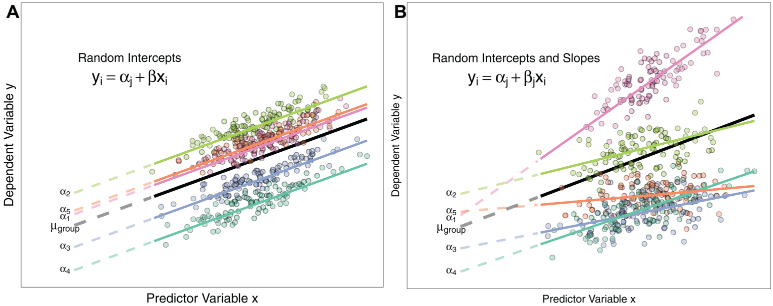
Random intercepts and random slopes:



Harrison et al. 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ, 6, p.e4794.

Mixed models

$$f_i^u(s) \propto \exp(x_1(s)\beta_{1i} + x_2(s)\beta_{2i} + \ldots x_p(s)\beta_{pi})$$

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$$(\beta_{1i}, \ldots, \beta_{2i}) \sim N(\mu, \psi)$$

Similar 2-step approach, but assume the regression parameters come from a common normal distribution.

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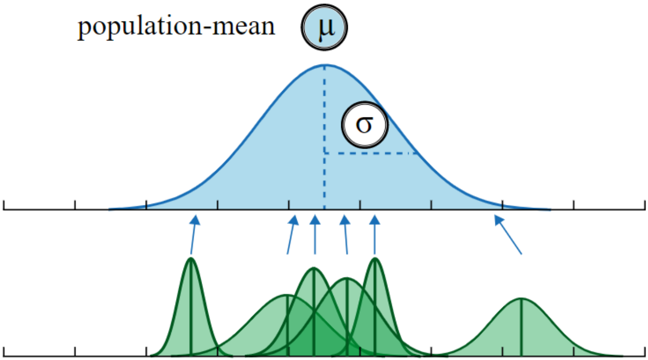
- inference at individual- and population-level with single model
- can “borrow strength” across individuals when estimating $(\beta_{1i}, \ldots, \beta_{2i})$
- can estimate μ, ψ while accounting for sampling variability

Individual Estimates Borrow Strength (Exhibit Shrinkage)



https://benediktehinger.de/glm2018/mm_slides.html

Downside of Random Effects

- More assumptions (parameters are normally distributed)
- Added complexity (requires numerical integration to calculate the likelihood), computationally challenging to fit
- Potentially more difficult for practitioners to understand, correctly specify, and communicate

Random Effects and Habitat-selection Models

Resource-selection functions:

- logistic regression with random effects, lots of options (e.g., `glmer` in `lme4` package)

Random Effects and Habitat-selection Models

Resource-selection functions:

- logistic regression with random effects, lots of options (e.g., `glmer` in `lme4` package)

Step-selection functions:

- conditional logistic regression, few good options
- `coxme` for small numbers of strata (SLOW!)
- `TwoStepCLogit::Ts.estim()`, a formal two-step approach (will fail if some individuals do not experience all levels of a categorical variable)

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BIOLOGGING

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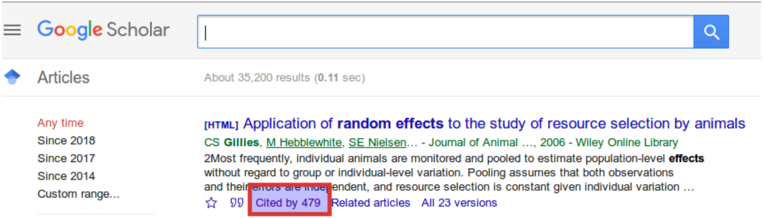
- How are random effects used in applications of RSFs?
- Develop computationally efficient method of fitting SSFs with random effects

One Step: Random Effects

- Random effects were proposed for RSFs over 10 years ago[1]



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One Step: Random Effects

- Random effects were proposed for RSFs over 10 years ago[1]

- Majority of studies (80 % since 2016) only include random intercept and no random slope(s).

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RSFs: Random Intercept-Only Models

1. Intercept in RSFs is not of interest and depends heavily on the sampling ratio of used versus available points

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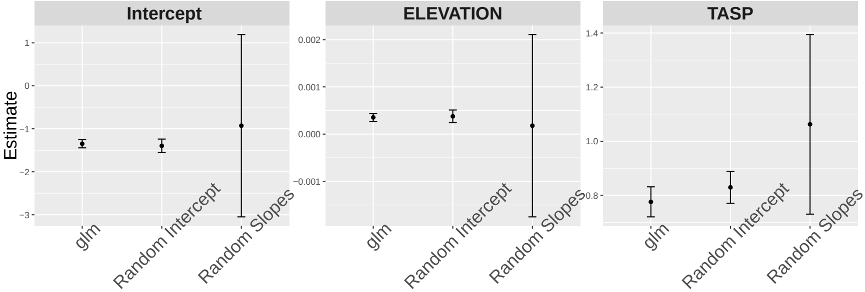
2. Cannot (by definition) account for among-animal variation in the regression slopes (i.e., functional responses)!

3. SEs will be too small, particularly with lots of observations for each animal

Schielzeth, H. and W. Forstmeier (2009). Conclusions beyond support: Overconfident estimates in mixed models. Behavioral Ecology 20, 416-420.

Example: Goat RSFs

```
glm <- glm(STATUS ~ TASP + ELEVATION, family=binomial(),
          data = goats)
glmer_int <- glmmTMB(STATUS ~ TASP + ELEVATION + (1|ID),
                    family=binomial(),data = goats)
glmer_randcoef <- glmmTMB(STATUS ~ TASP + ELEVATION +
                         (1+TASP+ELEVATION|ID),
                         family=binomial(), data = goats)
```



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

Computationally Efficient Step-Selection Functions

How can we fit SSFs with random effects?

Computationally Efficient Step-Selection Functions

How can we fit SSFs with random effects?

Reformulate SSFs as a Poisson model with stratum-specific intercepts α_{nt} (Armstrong et al. 2014):

- Same likelihood kernel as condition logistic regression likelihood, same $\hat{\beta}$, same SE($\hat{\beta}$)
- Treat intercepts as random with large fixed variance: $\alpha_{nt} \sim N(0, 10^6)$ (avoids shrinkage)
- Options: `glmmTMB` or `INLA` (Bayesian)

Armstrong et al. 2014. Conditional Poisson models: a flexible alternative to conditional logistic case cross-over analysis. BMC medical research methodology 14:122.

Statistical Properties

Simulation study (SSFs):

- verify that the Poisson trick works, but only when fixing the variance of the random intercepts!
- compare models assuming independence, mixed-effect Poisson glmm, formal two-step approach

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Applied example (RSFs and SSFs):

- compare two-step and mixed-effect approaches

Applied Example

SSF: Simulation Study

Simulate movements of 20 animals according to a biased random walk

Candidate locations:

- Step-lengths: $\sim$ exponential(λ = 1)
- Turn angles: uniform($-\pi, \pi$)

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Candidate locations:

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Select among candidate locations with probability:

$$w(x) \propto \exp(x_1\beta_1 + x_2\beta_2 + x_1 b_{1i} + x_2 b_{2i})$$

- x_1 and x_2 measure habitat quality and elevation
- β_1 and β_2 are fixed effects
- b_{1i} and b_{2i} are random effects: $(b_{1i}, b_{2i}) \sim N(0, \psi)$

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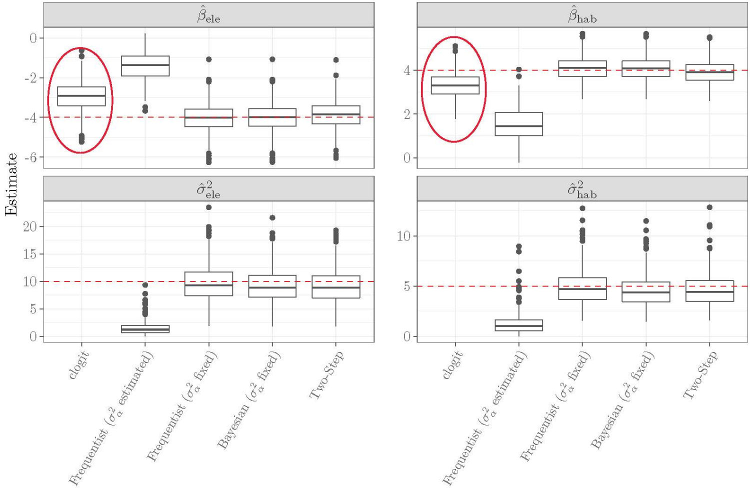
5. **Formal two-step approach**: using `Ts.estim()`

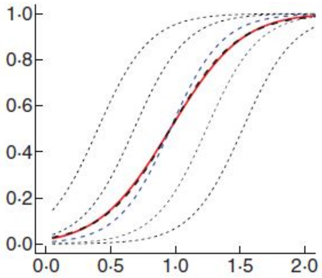
Fixed Effects Only (Attenuation Bias)



Population Averaged vs. Subject Specific

- clogit (pooled data): estimates a response curve for the population
- mixed model (setting all random effects = 0): estimates a response pattern for a 'typical individual'

These are not the same!

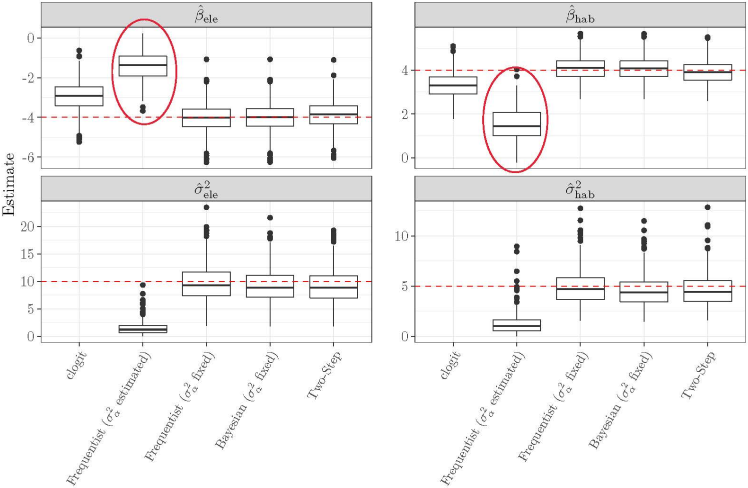


Muff, S., Held, L., & Keller, L. F. (2016). Marginal or conditional regression models for correlated non-normal data?. Methods in Ecology and Evolution, 7(12), 1514-1524.

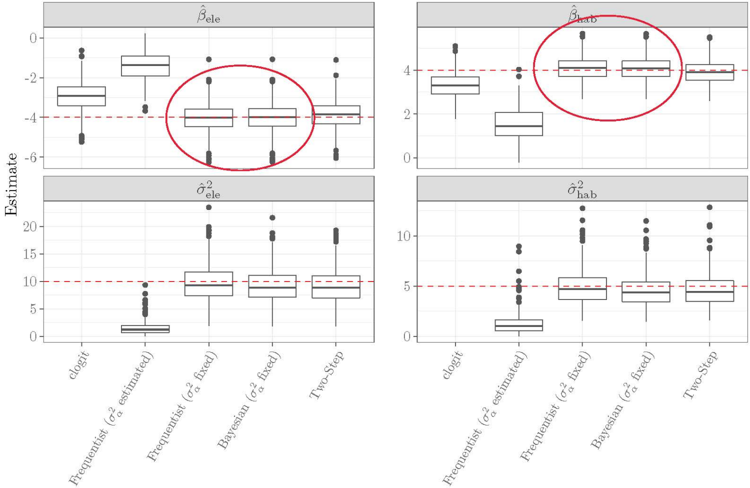
Fieberg, J., Rieger, R.H., Zicus, M. C., Schildcrout, J. S. 2009. Regression modelling of correlated data in ecology: subject specific and population averaged response patterns. Journal of Applied Ecology 46:1018-1025.

Fieberg, J., J. Matthiopoulos, M. Hebblewhite, M.S. Boyce, J. L. Frair. 2010. Correlation and studies of habitat selection: problem, red herring, or opportunity? Philosophical Transactions of the Royal Society, Series B 365:2233-2244.

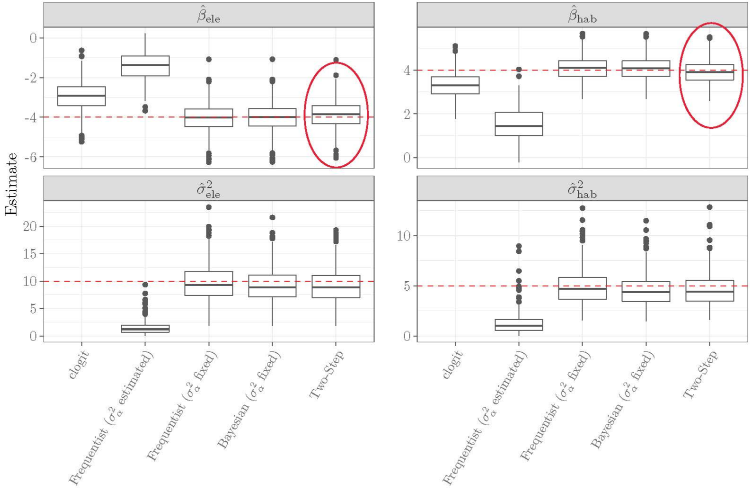
Random Effects with Estimated Intercept Variance



Random Effects with Fixed Large Variance

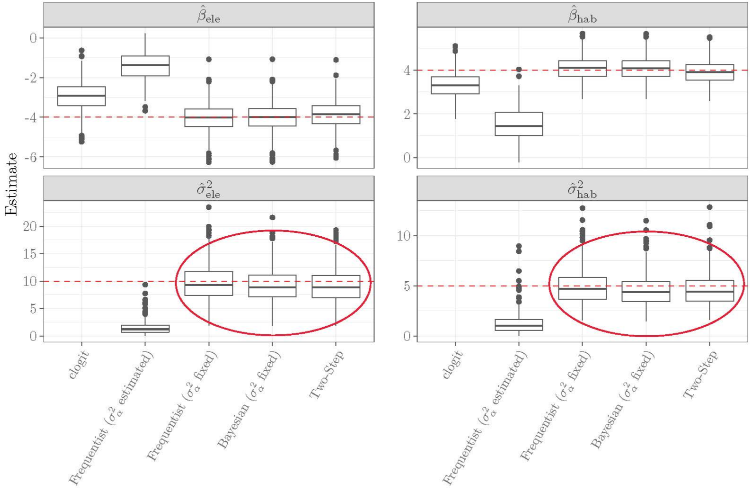


Two-step



$\hat{\beta}_{\text{ele}}$
$\hat{\beta}_{\text{hab}}$
$\hat{\sigma}^2_{\text{ele}}$
$\hat{\sigma}^2_{\text{hab}}$
Estimate
0
-2
-4
-6
4
2
0
20
15
10
5
0
10
5
0
clogit
Frequentist (σ^2_α estimated)
Frequentist (σ^2_α fixed)
Bayesian (σ^2_α fixed)
Two-Step

Variance Parameters



Applied Example

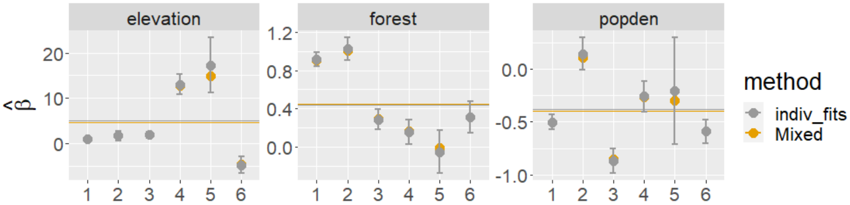
Covariates:

- elevation
- population density
- forest (yes/no)

Compare two-step approaches and mixed models:

- estimates of individual coefficients
- mean and variance of the coefficients across animals

Resource-Selection Functions



Variance estimates	sd($\beta_{\text{elevation}}$)	sd(β_{popden})	sd(β_{forest})
naive two-step (indiv_fits)	8.35	0.352	0.428
mixed model	7.07	0.315	0.382

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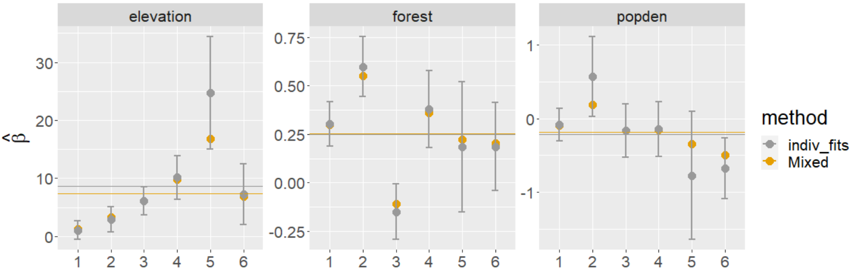
- likelihood weighting using estimates of effective sample size has been suggested as a way to deal with within-individual autocorrelation (Alson et al. in review. Mitigating pseudoreplication and bias in resource selection functions with autocorrelation-informed weighting)
- two-step approach + bootstrap (resampling individuals) could relax the assumption of independence within an individual

Step-Selection Functions



Variance estimates	sd($\beta_{\text{elevation}}$)	sd(β_{popden})	sd(β_{forest})
naive two-step (indiv_fits)	7.67	0.465	0.282
mixed model	4.91	0.293	0.252

Step-Selection Functions

Here, there are clear advantages to using mixed-model:

- beneficial shrinkage (due to smaller sample sizes since we are modeling transitions requiring equally-spaced time points)
- estimates of variance parameters are not biased by sampling variability
- BUT: steps may still be autocorrelated depending on the sampling frequency

Next steps

We will explore code for:

- implementing a two-step approach using tidyverse principles
- fitting mixed SSFs using glmmTMB (frequentist)
- fitting mixed SSFs using INLA (Bayesian)

Some FAQs

- How many individuals are needed to estimate variance components?
  - Is it OK to assume coefficients vary independently `(0 + x1|id) + (0 + x2|id)`?

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- Is it OK to assume turn angles and step lengths are independent?
- Should we incorporate longer-term dependencies, and if so, how?
- How should we account for changes in animal movement and habitat selection patterns?
  - over time (diurnally, seasonally)
  - across different behavioral states