How to Analyze Data From Multiple Animals

John Fieberg, Associate Professor

Department of Fisheries, Wildlife and Conservation Biology

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    - RSFs
    - SSFs

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2. We may want to know what is driving any differences among animals
3. We may want to pool information across individuals to better understand population-level selection patterns

Causes of Individual Variability

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Volume 26, Issue 2
March-April 2015

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

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,
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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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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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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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Functional Response in Habitat Selection

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What would you expect to see if you plotted animal-specific RSF parameters against availability of that resource?

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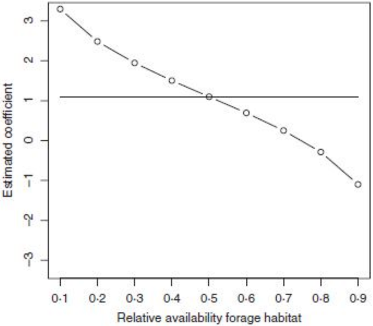

Aarts, G., Fieberg, J., Brasseur, S., & Matthiopoulos, J. (2013). Quantifying the effect of habitat availability on species distributions. Journal of animal ecology, 82(6), 1135-1145.

Methods for Modeling Data From Multiple Individuals

1. Fit models to pooled data, ignoring the fact that we have repeated measures, but use “robust SEs” (Generalized Estimating Equations or a “cluster-level bootstrap”) for inference

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3. Mixed models (aka hierarchical models, random effect models): allow parameters to vary by animal

Individual Variability is Important

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

Two-step Approach

Mixed models

Two-Step Approach

Step 1: fit models to individuals

$$f_i^u(s) \propto \exp(elev(s)\beta_i + popD(s)\gamma_i + forest(s)\tau_i)$$

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- relate coefficients to animal-specific characteristics (e.g., age, sex) using say `lm`
- plot coefficients against availability to explore functional responses

Fit models to individual animals

- 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.

Two-step Approach

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

```
## # A tibble: 8 x 7
##   id        n Elevation  forest `log(sl_)`   PopDens       sl_
##   <fct> <int>     <dbl>   <dbl>      <dbl>     <dbl>     <dbl>
## 1 F1     6391    0.0337  17.4        0.751 -0.00208   0.00272
## 2 F2    22165    0.0467  -0.274      0.687 -0.00112  -0.00338
## 3 F3    10169    0.0868  -0.591      0.603 -0.00225   0.000765
## 4 M1     4697    0.0776  -0.219      0.510  0.000583  0.00352
## 5 M2    10709    0.0292  -0.258      0.441 -0.00258   0.00193
## 6 M3    15547    0.0485   0.470      0.532 -0.00157   0.00272
## 7 M4    54810    0.0153   0.213      0.644 -0.000511  0.00197
## 8 M5    52303    0.00350 NA          0.848 -0.0232    0.00444
```

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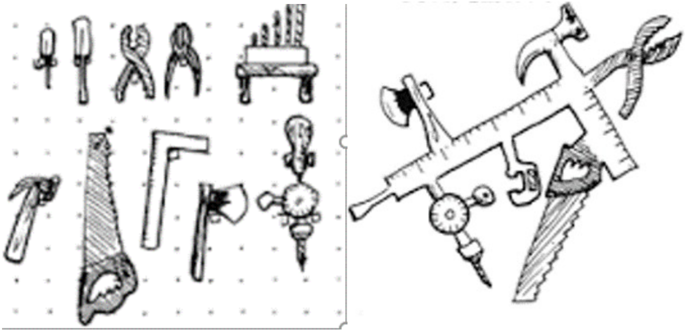
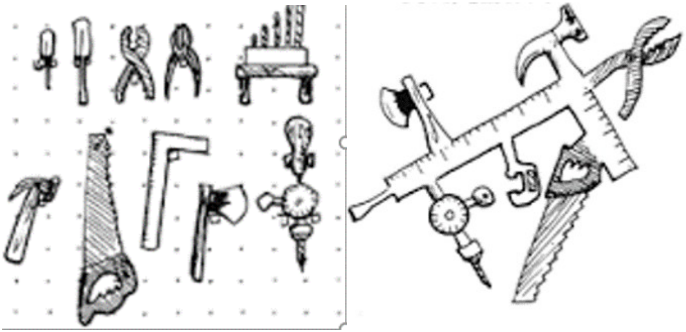
But. . . more assumptions, added complexity

Two-step versus Mixed Effects Models



Two-step versus Mixed Effects Models



"If you can't explain it simply, you don't understand it well enough" - Albert Einstein

Random Effects and Models of Habitat Selection

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

[1] 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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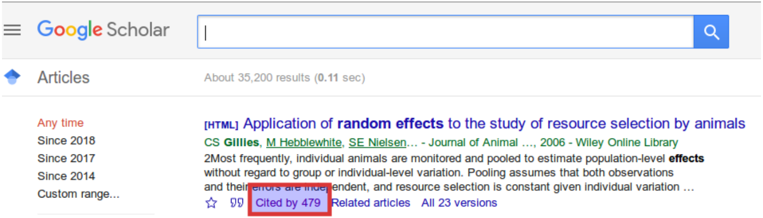

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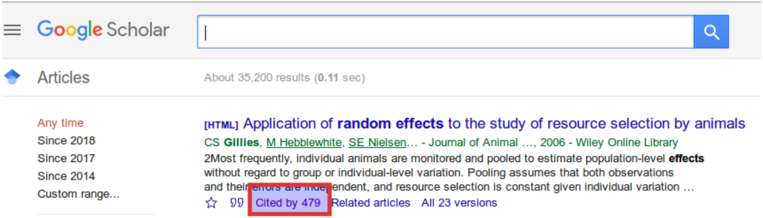

- Majority of studies (80 % since 2016) only include random intercept and no random slope(s).

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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

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

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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[5]

---

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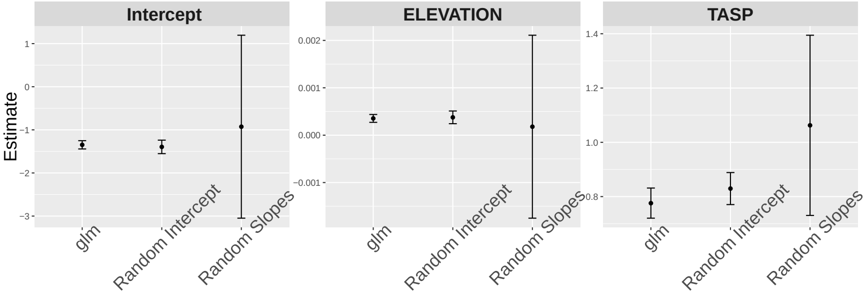
Example: Goat RSFs[6]

```
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)
```



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

SSFs: Mixed Effects

Conditional logistic regression with random effects is computationally prohibitive for most data sets.

Options:

- `coxme` for small numbers of strata
- `TwoStepCLogit::Ts.estim()`, a two-step approach

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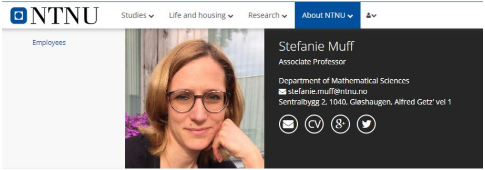
BIOLOGGING

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

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]



Norwegian University of Science and Technology

Mixed SSF Trick

Reformulation SSFs as a Poisson model with stratum-specific intercepts α_{nt}[5]

- Same likelihood kernel as condition logistic regression likelihood, same $\hat{\beta}$, same SE($\hat{\beta}$)

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- But, then lots of intercepts to estimate (one for every used location!)
- Trick: $\alpha_{nt} \sim N(0, 10^6)$ (avoids shrinkage and explicit estimation)

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Applied Example

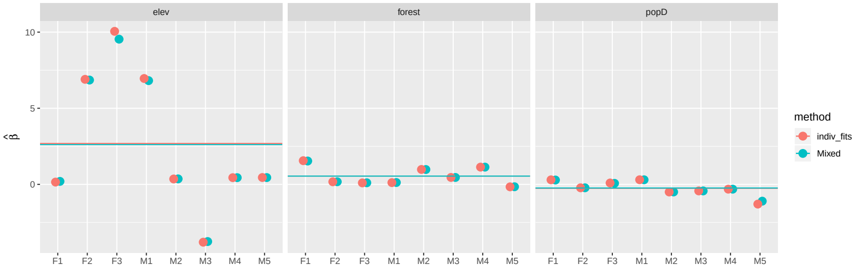
Covariates:

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

Compare two-step approaches and mixed models:

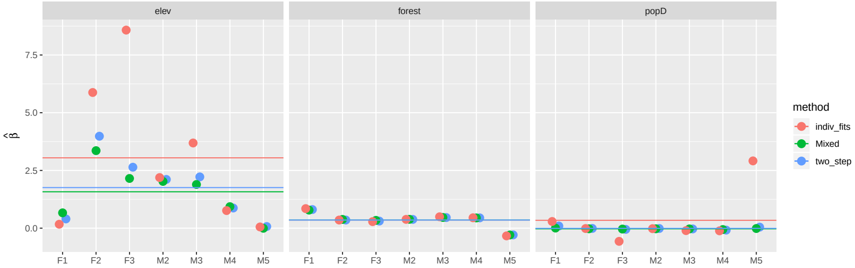
- individual estimates
- estimated mean coefficients
- estimated variance of the coefficients across animals

RSFs



Variance estimates	sd(β_{ele})	sd(β_{popD})	sd(β_{forest})
naive two-step (indiv_fits)	4.69	0.523	0.608
mixed model	4.21	0.443	0.564

SSFs



Variance estimates	sd(β_{ele})	sd(β_{popD})	sd(β_{forest})
naive two-step (indiv_fits)	2.49	1.02	0.339
formal two-step ('TS.Estim')	1.67	0.036	0.228
mixed model	1.35	0.0000019	0.312

Summary

Naive two-step approach:

- simple and easy to understand
- estimators of variance components biased high

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Poisson trick:

- fast, can estimate variance components (and their uncertainty), can share information across individuals
- formal one-step framework for fitting mixed-effect RSFs and SSFs

Implementation

- Two-step methods: tidyverse and via Ts.estim
- Frequentist mixed models: glmmTMB

See paper and associated code for a Bayesian implementation using INLA and Stan.